



Utilising wild genetic diversity for climate-resilient moth bean (*Vigna aconitifolia* (Jacq.) Maréchal) improvement through introgression breeding: A review

S Kaviya Shree¹, S Saravanan^{2*}, S Juliet Hepziba¹, J Sheela³ & A Kavitha Pushpam⁴

¹Department of Genetics and Plant Breeding, V.O. Chidambaranar Agricultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Killikulam 628 252, Tamil Nadu, India

²Cotton Research Station, Tamil Nadu Agricultural University (TNAU), Srivilliputhur 626 135, Tamil Nadu, India

³Department of Plant Pathology, V.O. Chidambaranar Agricultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Killikulam 628 252, Tamil Nadu, India

⁴Department of Crop Physiology and Biochemistry, V.O. Chidambaranar Agricultural College and Research Institute, Tamil Nadu Agricultural University (TNAU), Killikulam 628 252, Tamil Nadu, India

Correspondence: S Saravanan, saravananspbg@tnau.ac.in

Abstract

Moth bean (*Vigna aconitifolia* (Jacq.) Maréchal) is an underutilised, climate-resilient grain legume well adapted to the arid and semi-arid regions of the Indian subcontinent. Despite its exceptional tolerance to drought and heat, its genetic improvement has been constrained by a narrow-cultivated gene pool, limited genomic resources and the underutilisation of wild relatives. As climate change increases the occurrence of abiotic and biotic stresses, broadening the genetic base of moth beans has become essential for developing resilient and high-yielding cultivars. This review critically examines the potential of introgression breeding as a strategic approach for incorporating beneficial alleles from wild *Vigna* species, including *Vigna trilobata* (L.) Verdc., *Vigna stipulacea* (Lam.) Kuntze, *Vigna indica* T.M.Dixit, K.V.Bhat and S.R.Yadav and *Vigna aridicola* N.Tomooka & Maxted. Previous reviews have primarily emphasised the nutritional value, genetic diversity and general breeding potential of moth bean, with limited focus on systematic wild relative utilisation and introgression pathways. In contrast, this review integrates wild gene-pool classification, donor-trait relationships, reproductive barriers, linkage drag, pre-breeding strategies and genomics-assisted approaches within a unified breeding framework. It further evaluates the application of marker-assisted backcrossing, advanced backcross quantitative trait loci analysis (QTL), comparative genomics, genomic selection and emerging molecular tools for efficient trait introgression. The synthesis indicates that combining systematic donor characterisation with reproductive barrier management, precision introgression and validated genomic tools can accelerate the deployment of adaptive alleles from wild relatives. Future breeding efforts should prioritise multi-environment validation, high-throughput phenotyping, cost-effective genotyping and targeted utilisation of wild germplasm to broaden the genetic base and develop climate-resilient moth bean cultivars.

Keywords: climate resilience; genetic diversity; introgression; moth bean; pre-breeding; wild relatives

Received: 17 July 2026. **Accepted:** 09 September 2026. **Published:** Version 1.0: 17 October 2026.

Cite this article: Kaviya SS, Saravanan S, Juliet HS, Sheela J, Kavitha PA. Utilising wild genetic diversity for climate-resilient moth bean (*Vigna aconitifolia* (Jacq.) Maréchal) improvement through introgression breeding: A review. Plant Science Today. 2026; 13(sp9): 1-18. <https://doi.org/10.14719/pst.16828>

1. Introduction

The Green Revolution enabled India to attain self-sufficiency in food-grain production, marking a landmark achievement in agricultural development (1). However, long-term dependence on a narrow range of high-yielding staple crops has exposed structural weaknesses in the production system, including declining soil quality, increased pest and disease incidence, rising input costs and uneven regional development, collectively eroding agricultural sustainability (2). These challenges are compounded by reduced crop diversification and the widespread cultivation of genetically uniform varieties,

which facilitate the emergence of novel pests and pathogens and further weaken agroecosystem resilience. With limited scope for expanding cultivable land, these constraints intersect with rapid population growth and rising food demand; national food requirements are projected to increase substantially by the mid-twenty-first century as India's population approaches 1.6 billion (3). Recent global assessments similarly identify land degradation, biodiversity loss and socioeconomic inequalities as major pressures on agrifood systems, threatening progress toward zero hunger by 2030 without transformative action (4).

The increasing difference between food demand and climate constrained agricultural output highlights the inadequacy of input intensive, cereal centric farming models to ensure long-term self-sufficiency. To overcome these challenges, there is a need for a strategic transition toward diversified and resilient cropping systems. In this regard, underutilised crop species assume renewed importance, as many were cultivated extensively in the past or possess significant potential for wider adoption but remain marginalised due to agronomic, economic or genetic limitations (5). Among these, legumes occupy a pivotal position in sustainable agriculture due to their inherent capacity for biological nitrogen fixation. However, their productivity remains disproportionately vulnerable to abiotic stresses intensified by climate change (6). These underexploited crops, particularly legumes, harbour rich genetic variability. They combine adaptive traits for stress tolerance with improved nutritional quality. Their targeted enhancement and integration into mainstream agriculture, especially through introgression-based breeding strategies, can broaden the crop base, improve system resilience and contribute meaningfully to sustainable food and nutritional security under changing climatic conditions.

Among underutilised legume crops, moth bean (*Vigna aconitifolia* (Jacq.) Maréchal; $2n = 2x = 22$) belongs to the Fabaceae family and remains largely overlooked despite its remarkable adaptability to harsh, resource limited environments. It is commonly known as matki, mat bean, dew bean, Turkish gram or haricot papillon (7). Beyond its adaptability, moth bean plays a multifunctional role in small holder farming systems. In addition to providing protein rich grains, its sprouts and tender pods are consumed as vegetables (8). When consumed alongside cereals, it improves dietary quality by supplying essential amino acids that are limited in cereal based diets (9). This minor legume has traditionally been cultivated in the hot and dry regions of the Indian subcontinent, where low rainfall and high temperatures severely constrain the performance of most conventional legumes (7). Its continued cultivation in these regions reflects its inherent stress adaptation rather than dependence on intensive agronomic inputs.

This inherent resilience, coupled with its nutritional value and sustainability for marginal environments, positions moth bean as a promising crop for strengthening climate adaptive agriculture (10). Despite its ecological fitness, genetic improvement in this species has been limited by a narrow cultivated gene pool and underutilisation of wild and related species. Under accelerating climate stress, conventional breeding alone is unlikely to unlock the full adaptive potential required for sustained yield stability. Introgression breeding offers a powerful pathway to enrich the gene pool by incorporating desired alleles from wild relatives, thereby enhancing tolerance to abiotic and biotic stresses without compromising agronomic performance (11). Recent advances in molecular and pre-breeding tools have further enhanced

the efficiency of this approach. Therefore, understanding introgression pathways in moth bean is critical for developing climate-resilient cultivars. Although several studies have explored the stress resilience and genetic resources of moth bean, research on the wild relative utilisation, pre-breeding and genomics assisted introgression has remained largely absent. This review integrates these aspects and provides a comprehensive perspective on utilising wild *Vigna* diversity to accelerate climate-resilient moth bean improvement.

Methodology

A systematic literature search was conducted to identify and compile published information on the use of wild relatives for the genetic improvement of moth bean (*Vigna aconitifolia* (Jacq.) Maréchal), with particular emphasis on introgression breeding, genetic diversity, climate resilience and genomics-assisted breeding approaches. The review was performed following the preferred reporting items for systematic reviews and meta-analyses (PRISMA) framework to ensure a transparent and reproducible literature selection process (Fig. 1).

Scientific literature was retrieved from Web of Science, Scopus, PubMed, Google Scholar and additional sources, including reference lists, theses and manual searches. The search covered publications from January 1970 to May 2026 and the final search was conducted on 28 May 2026. The year 1970 was selected as the starting point because it corresponds to the earliest available indexed literature on moth bean identified in the databases searched. Searches were performed using combinations of keywords related to the crop, wild genetic resources, breeding approaches and stress tolerance, including “moth bean”, “*V. aconitifolia*”, “wild relatives”, “crop wild relatives”, “gene pool”, “genetic diversity”, “introgression breeding”, “pre-breeding”, “marker-assisted backcrossing”, “genomic selection”, “comparative genomics”, “drought tolerance”, “heat tolerance”, “biotic stress”, “abiotic stress”, “reproductive barriers”, “embryo rescue” and “*Vigna* wild species”. The principal Boolean search strategy combined these terms using the following conceptual search string: (“moth bean” OR “*Vigna aconitifolia*”) AND (“wild relatives” OR “crop wild relatives” OR “wild species” OR “gene pool”) AND (“genetic diversity” OR “introgression breeding” OR “pre-breeding” OR “marker-assisted backcrossing” OR “genomic selection” OR “comparative genomics”) AND (“drought tolerance” OR “heat tolerance” OR “biotic stress” OR “abiotic stress” OR “reproductive barriers” OR “embryo rescue”). Additional relevant publications were identified through citation tracking and manual screening of reference lists.

Study selection was performed in two stages. Initially, titles and abstracts were screened to identify studies relevant to moth bean, *Vigna* wild relatives, genetic diversity, introgression breeding, pre-breeding, climate-related stress tolerance, reproductive barriers,



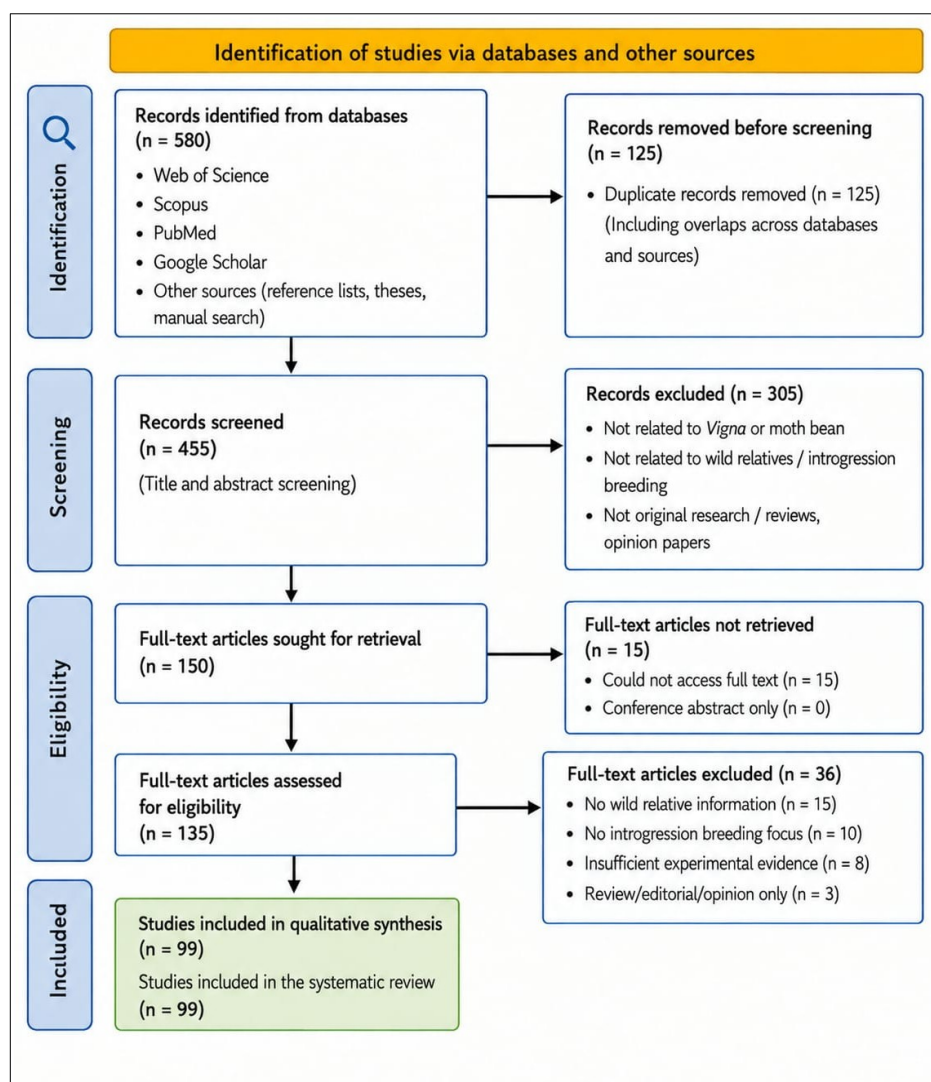


Fig. 1. Preferred reporting items for systematic reviews and meta-analyses (PRISMA)-style flow chart.

or genomics-assisted breeding. Potentially relevant publications were subsequently evaluated through full-text screening against predefined inclusion and exclusion criteria. Studies were considered relevant when they provided information directly related to the utilisation or characterisation of moth bean and its wild relatives, genetic diversity, gene pools, interspecific hybridisation, introgression or pre-breeding strategies, reproductive barriers, molecular or genomic approaches or stress tolerance traits relevant to climate-resilient crop improvement. The scientific quality and relevance of the included literature were assessed based on the clarity of the study objectives, adequacy of the experimental or methodological description, relevance of the genetic material or species investigated, availability of supporting experimental or genetic evidence, clarity of the reported results and consistency between the reported results and conclusions. Studies with insufficient methodological or experimental information, limited relevance to the objectives of the review or inadequate scientific evidence were excluded. Owing to the heterogeneous nature of the literature, which included experimental studies, genetic diversity

assessments, breeding studies, genomic analyses and relevant review and methodological publications, no formal numerical risk-of-bias scoring system was applied.

A total of 580 records were identified from all sources. Following the removal of 125 duplicate records, 455 articles were screened based on their titles and abstracts. Articles unrelated to *Vigna* or moth bean, studies not focusing on wild relatives or introgression breeding and publications lacking original scientific information were excluded during the screening stage. Subsequently, 150 full-text articles were sought for detailed evaluation. Of these, 15 articles could not be retrieved due to lack of full-text availability or because only conference abstracts were accessible. The remaining 135 full-text articles were assessed for eligibility using predefined inclusion and exclusion criteria. After full-text evaluation, 40 articles were excluded because they lacked relevant experimental evidence, did not focus on introgression breeding or wild relatives, or did not meet the predefined eligibility criteria. Finally, 99 studies were included in the qualitative synthesis following the PRISMA 2020 guidelines.

Information extracted from the selected studies was critically evaluated and organised into thematic sections covering the taxonomy and domestication of moth bean, genetic diversity, wild relatives, introgression breeding strategies, reproductive barriers, molecular breeding approaches and future perspectives for the development of climate-resilient moth bean cultivars.

Botanical, genetic and physiological foundations of moth bean

Scientific identity, taxonomy and phylogeny

Moth bean (*V. aconitifolia*) is a diploid ($2n = 2x = 22$) annual grain legume belonging to the family Fabaceae and subfamily Papilionoideae. It was initially described under the genus *Phaseolus*, but later reassigned to the genus *Vigna*, tribe Phaseoleae based on molecular characteristics and phylogenetic evidence (12). Within the genus, moth bean is classified under the Asian *Ceratotropis* subgenus, which includes important pulses such as *Vigna radiata* (L.) R. Wilczek and *Vigna mungo* (L.) Hepper (9). This taxonomic replacement is further supported by evolutionary evidence. Phylogenetic analyses based on nuclear and chloroplast DNA markers indicate that moth bean is closely related to other Asian *Vigna* species but remains genetically distinct. This distinctiveness suggests independent domestication and adaptive divergence within the group (13). From a genomic perspective, moth bean possesses a relatively compact genome, estimated at approximately 360–380 Mb, with a substantial proportion comprising repetitive elements (14). Its diploid nature and conserved chromosomal organisation make it a suitable candidate for comparative genomics and facilitate introgression within the *Ceratotropis* group.

Morphologically, moth bean is an annual crop characterised by a spreading to semi-erect growth habit with profuse branching, while its trailing stems often extend along the soil surface to form a dense canopy (15). This growth habit represents an adaptive response to arid environments by reducing soil moisture and minimising wind erosion in sandy soils (9). The leaves are trifoliate with variable leaflet morphology, whereas the flowers are yellow, papilionaceous and borne in axillary clusters. The pods are short and contain several small seeds, with substantial variation in seed size and seed coat colour observed across genotypes, reflecting the considerable morphological diversity within the species. This morphological diversity also extends to plant architecture and pod traits among landraces and improved cultivars, reflecting the combined effects of natural selection under stress-prone environments and domestication influences (16). Phenologically, moth bean is predominantly cultivated during the kharif season under rainfed conditions in India and performs well under temperatures ranging from 25–37 °C, limited to moderate rainfall (9). Genotypic variation in flowering time and maturity duration contributes to adaptation under short growing seasons and erratic rainfall conditions. Although domestication has favoured reduced dormancy and improved reproductive efficiency, many cultivars continue

to exhibit partial indeterminacy, resulting in staggered flowering and maturity (15).

Origin and domestication

Genetic diversity analysis and archaeological evidence collectively support India as the primary centre of origin and domestication for moth bean (17). Subsequent diversification across South Asia has been significant, with Sri Lanka and Pakistan identified as important reservoirs of genetic variation, reflecting the crop's broader evolutionary history in the region (18). From this South Asian centre, moth bean gradually expanded into neighbouring countries such as Bangladesh, Myanmar and China, where it demonstrated strong adaptation to semi-arid agroecological conditions (19). Within India, the crop is predominantly concentrated in Rajasthan, widely regarded as the country's driest state and the largest contributor to its cultivated area. This distribution pattern reflects moth bean's resilience in arid climates and highlights its agronomic importance in sustaining dryland farming systems (20).

The long-term cultivation of moth bean in diverse and stress prone environments has not only shaped its geographical distribution but also influenced its domestication and genetic structure. Domestication of moth bean likely involved gradual selection for traits such as increased seed size, improved pod retention, reduced dormancy and earlier flowering. However, compared with major pulse crops, it has undergone limited systematic breeding, resulting in a relatively narrow cultivated gene pool (21). Continuous adaptation to arid and semi-arid climates further shaped its genetic structure, favouring genotypes capable of surviving under moisture stress and high temperature (9).

Physiological basis of stress adaptation and agroecological distribution

The physiological robustness of moth bean underpins its recognition as a climate-resilient pulse crop. One of its prominent adaptive features is a deep and efficient taproot system that enables access to moisture from deeper soil layers during prolonged dry spells (9). In addition, its spreading canopy architecture contributes to stress mitigation by lowering soil surface temperature and reducing evapotranspiration losses (15). Moth bean also exhibits notable tolerance to high temperatures, maintaining reproductive stability under heat stress conditions typical of semi-arid regions (16). Such thermotolerance supports its cultivation in environments where many other pulse crops experience substantial yield reduction. As a legume, moth bean forms symbiotic associations with nitrogen-fixing rhizobia, enabling efficient biological nitrogen fixation in nutrient poor soils (9). This characteristic enhances soil fertility and supports low-input production systems.

Geographically, moth bean is primarily cultivated in the arid and semi-arid regions of northwestern India, particularly Rajasthan and Gujarat, where rainfall is sparse and erratic (16). It performs well in sandy and sandy loam soils with low organic content and under rainfall of approximately 250–500 mm (15).



Its ability to complete its life cycle under moisture deficit and high temperature conditions highlights its ecological efficiency. Together, deep rooting ability, canopy mediated moisture conservation, thermotolerance and nitrogen fixation form the physiological backbone of moth bean's adaptation to marginal environments.

Genetic diversity and domestication bottlenecks in moth bean

Narrow genetic base and consequences of domestication

Domestication and long-term cultivation of moth bean have resulted in a relatively narrow genetic base within the cultivated gene pool, thereby limiting the potential for genetic improvement through conventional selection methods (22). Recent genotyping-by-sequencing analysis of a diversity panel comprising 428 accessions revealed a distinct population structure and limited allelic variation among cultivated lines. These findings highlight the need to broaden the genetic base through the incorporation of diverse and exotic germplasm (23).

Despite recent progress in the development of transcriptomic resources and molecular markers, genomic resources in moth bean remain comparatively underdeveloped. High-quality reference genome assemblies, high density linkage maps and comprehensive trait mapping studies are still limited, restricting the precise identification and deployment of alleles associated with key agronomic traits (23). Consequently, greater emphasis has been placed on the strategic utilisation of wild germplasm resources together with genomics assisted breeding approaches to accelerate genetic gain and broaden the adaptive potential of this underutilised legume (24).

Molecular profiling of moth bean genetic diversity

Early studies provided the first structured insights into the genetic architecture of yield components and plant morphology (25). Subsequent advancements in next generation sequencing technologies have enabled genome-wide marker discovery in moth bean. A comprehensive genotyping-by-sequencing study involving 428 accessions identified a total of 9078 high-quality single nucleotide polymorphisms (SNPs), revealing distinct population structure and moderate genetic differentiation among cultivated and landrace accessions (23). Importantly, this study supported the first genome-wide association study (GWAS) for flowering traits in moth bean, marking a critical transition from diversity analysis to trait dissection in this orphan crop.

Despite these advances, the molecular infrastructure required for precision breeding remains limited. High-density linkage maps integrating SNP markers, fine-mapped QTL regions and functionally validated candidate genes are still lacking. Furthermore, the lack of chromosome scale reference genome restricts accurate marker positioning, haplotype analysis and comparative genomics. Such limitations constrain marker-assisted backcrossing, genomic selection and allele mining strategies (24, 26). In this context, comparative genomics within the genus *Vigna* offers a

practical strategy to bridge existing genomic gaps. Significant genomic collinearity has been reported among Asian *Vigna* species such as *V. radiata* and *Vigna unguiculata* (L.) Walp., suggesting that genomic resources from mungbean and cowpea can be effectively utilised for marker development, candidate gene prediction and comparative trait analysis in moth bean (24, 27). The exploitation of conserved orthologous QTL regions and cross-species transferable markers may accelerate introgression breeding while minimising linkage drag associated with wild donors (28, 29).

Further genetic improvement in moth bean will increasingly depend on the integration of advanced genomic approaches capable of capturing the polygenic nature of climate resilience traits. Genomic selection models incorporating genome-wide marker effects have already demonstrated considerable success in accelerating genetic gain in legumes such as chickpea and pigeonpea (30, 31). Similar approaches could substantially enhance breeding efficiency in moth bean once sufficiently large and well characterised training populations are developed. Beyond genomic prediction, multi-omics integration represents an important frontier for functional validation of candidate genes. Transcriptomic analysis under drought and heat stress conditions can elucidate regulatory networks governing stress adaptation, while metabolomic and proteomic analyses provide complementary insights into the physiological basis of resilience (30, 32). However, the application of advanced computational frameworks and machine learning approaches in moth bean remains constrained by limited curated genotype-phenotype datasets. This underscores the need for centralised genomic repositories and standardised phenotypic platforms (26, 33). Molecular and genomic resources available for moth bean are summarised in Table 1.

Diversity of wild relatives of moth bean

The wild relatives of moth bean mainly belong to the genus *Vigna* and the subgenus *Ceratotropis*, which represents the Asian lineage of *Vigna*. This group includes many wild and semi-domesticated types that show strong ecological adaptability and genetic diversity. Unlike most cultivated Asian *Vigna* species, moth bean lacks a formally recognised wild ancestor. The cultivated moth bean shows traits typical of wild plants, including indeterminate growth, pod shattering and seed dormancy. These characteristics suggest that the domestication process has been shallow (18, 25). All the known wild relatives of the moth bean are interspecific. Therefore, the relationship between these interspecific relatives and the moth bean has been investigated by molecular phylogenetics.

Vigna trilobata (L.) Verdc

Vigna trilobata is recognised as the closest wild relative of moth bean, sharing membership in section *Aconitifoliae* of subgenus *Ceratotropis* and possessing the same chromosome number ($2n = 22$) (13, 34). Molecular phylogenetic analyses based on ribosomal



Table 1. Molecular and genomic resources available for moth bean

Resource	Type	Details	Application in breeding	References
Marker systems				
SSR (microsatellite) markers	Co-dominant DNA markers	11 linkage groups, ~1016 cM total map length, 50 QTLs are mapped for yield, stress and phenology.	Foreground and background selection in MABC, linkage mapping and germplasm fingerprinting	(2)
SNP markers (GBS derived)	Single nucleotide polymorphisms via genotyping-by-sequencing	9078 high quality SNPs.	GWAS for drought, heat and disease resistance loci, used in population structure and diversity assessment	(23)
Genomic infrastructure				
Transcriptome / RNA-seq data	Gene expression profiling	Drought and heat stress transcriptomes available, identifies DREB, NAC, WRKY TF networks	Candidate gene identification, development of functional markers	(34)
Comparative genomics				
Synteny with mungbean	Comparative genomic mapping	High collinearity in gene order and marker positions, enables cross-species marker transfer	Predicts gene locations in moth bean using mungbean reference, accelerates marker development	(27, 33)
Synteny with cowpea	Comparative genomic mapping	Moderate collinearity and has a chromosome-scale reference genome available	Alternative reference for predicting QTL regions and candidate gene identification	

*cM: centimorgan; MABC: marker-assisted backcrossing; GWAS: genome-wide association studies; SNPs: single nucleotide polymorphisms; QTL: quantitative trait loci; DREB: dehydration-responsive element-binding protein; NAC and WRKY: transcription factors.

DNA-internal transcribed spacer (rDNA-ITS) sequences have placed *V. trilobata* in proximity to *V. aconitifolia* within section Aconitifoliae. Historically, *V. trilobata* was incorrectly proposed as the wild progenitor of moth bean. However, cytological, biochemical and molecular studies have since established these as distinct species (9, 35–37). Interspecific crosses between *V. aconitifolia* (female) and *V. trilobata* (male) confirm the feasibility of gene transfer between the two species through colchicine-induced amphiploidy (9, 38). *Vigna trilobata* is a well-documented donor of drought and heat tolerance traits, attributed to its deep taproot system that enables water extraction from deeper soil profiles during prolonged dry periods (39) and it is also tolerant to saline conditions (19). Additionally, *V. trilobata* harbours valuable variation for resistance to bruchid beetles (*Callosobruchus* spp.), foliar diseases and effective symbiotic nitrogen fixation. It is also traditionally valued as a green manure crop in semi-arid farming systems of South Asia (40, 41).

***Vigna indica* T.M.Dixit, K.V.Bhat & S.R.Yadav**

Vigna indica is a relatively underexplored wild species within the subgenus *Ceratotropis*. It is distributed across India and Southeast Asia in semi-arid and marginal environments. This indicates its adaptation to drought, heat and poor soils (42). Phylogenetically, it is more distant from *V. aconitifolia* than *V. trilobata* and is placed within the secondary to tertiary gene pool due to reproductive barriers (43, 44). Molecular evidence suggests a complex evolutionary origin, where rDNA-ITS data indicate close affinity with *V. aconitifolia*, while chloroplast (atpB-rbcL) sequences show similarity to

Vigna subramaniana (Babu ex Raizada) Raizada, supporting a possible interspecific hybrid origin of *V. indica* (13). Comparative genomics in *Vigna* further indicates the presence of stress-responsive alleles in gene families such as dehydration-responsive element-binding (DREB), NAM, ATAF and CUC (NAC) and WRKY transcription factor (WRKY), along with loci associated with osmotic regulation and heat tolerance (34, 45). These regions are often linked to quantitative trait loci (QTLs) governing drought tolerance and yield stability, although limited genomic resources restrict their utilisation. With advances in GWAS and pan-genomics, *V. indica* represents a promising donor for climate-resilient improvement of moth bean.

***Vigna stipulacea* (Lam.) Kuntze**

Vigna stipulacea is a closely related wild relative of moth bean (*V. aconitifolia*) and belongs to the same gene pool within the genus *Vigna*, making it suitable for use in interspecific hybridisation. Phylogenetic and molecular studies indicate a close evolutionary relationship among wild *Vigna* species, supporting their role as donors of beneficial traits (44). Importantly, *V. stipulacea* has been proposed as a promising candidate for neo-domestication due to its inherent tolerance to drought and its resistance to various diseases and pests (46). It exhibits broad-spectrum resistance to several biotic stresses (46), highlighting its potential as a genetic source for improving resistance to major diseases such as mungbean yellow mosaic virus (MYMV) (47) and powdery mildew in cultivated *Vigna* species (48). Additionally, *V. stipulacea* possesses a hard, water-impermeable seed coat that results in strong seed



dormancy, a typical wild trait that can be modified through mutagenesis to facilitate domestication (49). Due to its genetic proximity and adaptive traits, *V. stipulacea* is considered a valuable resource for pre-breeding and genetic improvement of *V. aconitifolia*.

***Vigna aridicola* N.Tomooka & Maxted**

Vigna aridicola is a wild *Vigna* species endemic to Sri Lanka (44). It is well adapted to continuously hot environments and exhibits a high degree of tolerance to dehydration (50). Alongside its abiotic stress resilience, it possesses resistance to important diseases such as brown stem rot and adzuki bean *Fusarium* wilt (51), making it a promising genetic resource for the improvement of both abiotic stress tolerance and disease resistance in cultivated *Vigna* species. Despite its tolerance to heat, dehydration and major pathogens, it remains relatively underexplored compared to other wild *Vigna* species. Detailed studies on its genetic diversity, crossability with cultivated forms and the identification of stress-associated genes or quantitative trait loci remain limited and require systematic investigation for effective utilisation.

***Vigna khandalensis* (Santapau) Raghavan et Wadhwa**

Vigna khandalensis, a near-threatened wild species, endemic to the Western Ghats of India (52), has been promoted as a potential “crop for the future” due to its resilience under marginal conditions and its traditional use as a famine food (53, 54). Phylogenetically, it exhibits moderate genetic relatedness with *V. aconitifolia*, highlighting its potential for utilisation in moth bean improvement (46). Notably, it is the only known erect growth type among wild *Vigna* species. It further exhibits intermediate heat tolerance and resistance to bruchids, enhancing its value as a genetic resource for enhancing stress resilience and storage pest resistance in cultivated *Vigna* species (6, 55).

Trait-by-donor matrix of cultivated and wild *Vigna* genetic resources for moth bean improvement is summarised in Table 2.

Trait introgression and pre-breeding strategies

Concept of introgression breeding

Introgression breeding refers to the transfer of desirable genes or QTLs from genetically diverse or wild species

into an adapted crop background through repeated hybridisation and backcrossing (61, 62). The concept originally termed “introgressive hybridisation” was introduced by Edgar Anderson and Leslie Hubricht in 1938 to describe the gene flow between species (63). This approach has gained considerable importance in crops such as moth bean, where the narrow genetic base of the cultivated germplasm limits the scope for improvement through conventional breeding approaches. Meanwhile, wild relatives adapted to diverse and extreme environments serve as valuable reservoirs of alleles with stress tolerance and resistance. Under changing climatic conditions, introgression breeding offers an effective means of enhancing resilience while retaining the desirable agronomic background of elite cultivars. As a result, it provides a promising pathway for improving yield stability and stress adaptation in moth bean (64).

Gene pool concept

The gene pool concept provides a useful framework for understanding how easily genes can be transferred between cultivated crops and their wild relatives. Based on the degree of crossability, related species are grouped into primary, secondary and tertiary gene pools, reflecting the ease of hybridisation and gene exchange (42). In moth bean (*V. aconitifolia*), the primary gene pool includes the cultivated species itself, where gene exchange occurs freely. The secondary gene pool (GP2) comprises closely related species such as *V. trilobata*, *V. indica*, *V. stipulacea* and *V. aridicola*, which can hybridise with moth bean but may show partial reproductive barriers. These species are particularly valuable as sources of traits like drought tolerance and disease resistance. In contrast, the tertiary gene pool (GP3) includes more distantly related species such as *V. khandalensis* and other *Vigna* species, where gene transfer is more difficult due to strong reproductive incompatibilities and often requires advanced techniques like embryo rescue or chromosome manipulation (42, 50). Understanding this classification helps identify suitable donor species. Yet, their effective utilisation requires systematic pre-breeding to overcome crossability barriers and undesirable wild traits. Gene Pool Classification and Crossability Relationships in Moth Bean and Its Wild Relatives is illustrated in Fig. 2.

Table 2. Trait-by-donor matrix of cultivated and wild *Vigna* genetic resources for moth bean improvement

Donor species	Donor accessions	Native distribution	Target trait	Experimental evidence	Candidate gene/ QTL/ Marker	Breeding application	References
<i>Vigna aconitifolia</i>	F2 population of cross TN67 × IPCMO056	India	Bruchid resistance	Artificial Bruchid infestation (% seed damage and QTL mapping)	<i>qVacBrc2.1</i> (<i>qVacBrc2.1-A</i> and <i>qVacBrc2.1-B</i>) and <i>qVacBrc5.1</i>	Backcross breeding, MABC.	(56, 57)
	IC-36522 and IC-36217	India	Yellow mosaic virus	Multi-location field screening based on Percent Disease Index (PDI)	-	Introgression breeding, Backcross breeding, MABC.	(58)



	IC-39786 and IC-39822	India	Leaf crinkle virus		-	Introgression breeding, Backcross breeding, MABC.	(58)
	IC-16218	India	Cercospora leaf spot		-	Introgression breeding, Backcross breeding, MABC.	(58)
	RMO-40	India	Drought tolerance	Drought induced phenotyping, CAT1 gene sequencing and phylogenetic analysis	Catalase (CAT1) gene	Introgression breeding	(59)
<i>Vigna trilobata</i>	JP205895	Sri Lanka	Drought tolerance	Relative Shoot biomass	-	Introgression breeding	(60)
	-	Southeast Asia	Heat tolerance	1–5 likert scale based on root/shoot biomass accumulation	-	Introgression breeding, MABC, Gene editing	(6)
	-	Southeast Asia	Salinity Tolerance	1–5 scale based on biomass accumulation, PSII quantum yield and leaf Na ⁺ /K ⁺ concentrations	-	MABC, Gene editing	(6)
<i>Vigna stipulaceae</i>	-		Heat tolerance	1–5 likert scale based on root/shoot biomass accumulation	-	MABC, Gene editing	(6)
	JP245503 mutant	India	Increased seed imbibition (isi1, isi2, isi3)	100 % seed imbibition within 1 hr; F ₂ segregation 221 WT: 59 mutant (≈3:1)	CesA7	Gene editing, gene pyramiding, de novo domestication	(49)
		India	Pod shattering (rps1)	Pod shattering reduced from 100 % (WT) to 0 %; pod twisting reduced from 0.866 to 0.371 twists/cm	-		(49)
<i>Vigna aridicola</i>	JP205894	Sri Lanka	Drought tolerance	Relative Shoot biomass	-	Introgression breeding	(60)
<i>Vigna vexillata</i> var. <i>ovata</i>	JP235908	South Africa	Drought tolerance	Relative Shoot biomass	-	Introgression breeding	(60)
<i>Vigna</i> sp. NI1135	JP110836	India	Drought tolerance	Relative Shoot biomass	-	Introgression breeding	(60)

MABC: marker-assisted backcrossing; GWAS: genome-wide association studies; QTL: quantitative trait loci; PDI: percent disease index; CAT1: catalase 1; PSII: photosystem II; Na⁺/K⁺: sodium/potassium ratio; WT: wild type; F₂: second filial generation; CesA7: cellulose synthase A7.



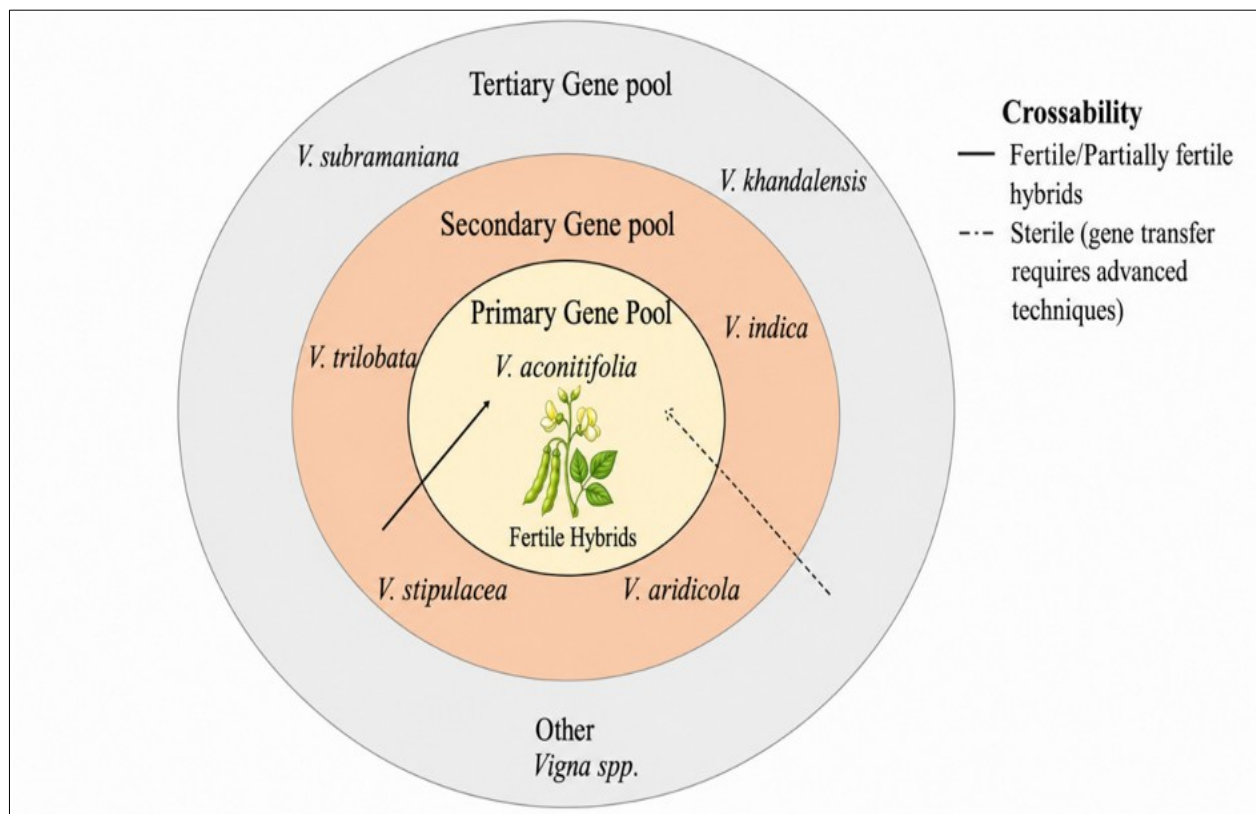


Fig. 2. Gene pool classification and crossability relationships in moth bean and its wild relatives.

Pre-breeding and germplasm utilisation

Pre-breeding refers to the identification of useful genes from wild relatives, landraces and other unadapted genetic resources that cannot be directly used in breeding programs and their transfer into intermediate materials that can be further utilised for crop improvement (65, 66). The term “pre-breeding” was introduced by Rick in 1984. In moth bean, pre-breeding assumes particular importance because the narrow genetic base of cultivated germplasm restricts the scope for genetic enhancement through conventional breeding approaches. Wild relatives within the *Vigna* genus, including *V. trilobata*, *V. stipulacea* and *V. indica*, serve as valuable germplasm resources as they possess adaptive traits such as drought tolerance, disease resistance and efficient nutrient utilisation (46, 64). However, their direct use in breeding is often constrained by undesirable wild characteristics such as seed dormancy, pod shattering and indeterminate growth habit.

Pre-breeding addresses these limitations through the development of intermediate materials such as interspecific hybrids and backcross-derived lines, which enable the gradual incorporation of desirable alleles into a cultivated background. These approaches help reduce linkage drag while improving the compatibility of wild traits with agronomic requirements (61). Thus, effective pre-breeding and germplasm utilisation are essential for harnessing the genetic potential of wild *Vigna* species and developing climate-

resilient moth bean cultivars. The integration of molecular markers into pre-breeding pipelines significantly enhances the efficiency of selection by enabling precise tracking of introgressed segments and identification of recombination events that break linkages between the target locus and unwanted genomic regions (67).

Introgression strategies for trait transfer

Backcross breeding

Backcross breeding is the most fundamental and widely used strategy for introgressing desirable traits from wild relatives into cultivated crops. It involves repeated crossing of hybrid progeny with a recurrent (elite) parent to recover its genetic background while retaining specific alleles from the donor parent (62). In moth bean, backcross breeding has been explored using closely related wild species such as *V. trilobata*, which serves as a valuable donor for genes associated with drought tolerance and adaptation to arid environments (64). The process typically begins with the formation of an interspecific hybrid, followed by successive backcross generations (BC_1 , BC_2 , etc.), where selection is applied to retain the target trait. However, conventional backcrossing has several limitations. The most significant is linkage drag, where undesirable traits such as pod shattering, small seed size, or indeterminate growth habit are co-transferred along with the target gene. In addition, the recovery of the recurrent parent genome is slow, often requiring 5–6 backcross

generations to achieve near-complete restoration (62). These limitations reduce its efficiency, particularly for complex traits such as drought and heat tolerance, which are controlled by multiple genes.

Marker assisted backcrossing

Marker-assisted backcrossing (MABC) is an advanced form of backcross breeding that utilises molecular markers to improve the precision and efficiency of introgression. By enabling direct selection at the DNA level, MABC significantly accelerates the recovery of the recurrent parent genome while ensuring the retention of target alleles (68). The MABC involves three key components. Foreground selection is used to identify individuals carrying the target gene or QTL. Background selection facilitates the recovery of the recurrent parent genome using genome-wide molecular markers. Recombinant selection helps minimise linkage drag by selecting recombination events occurring near the target locus. In moth bean, where genomic resources are still limited, markers from related *Vigna* species have been used to facilitate trait introgression, particularly for disease resistance and abiotic stress tolerance (24, 69). The use of MABC can reduce the number of required backcross generations to 2–3, compared to 5–6 in conventional methods. Despite its advantages, MABC is most effective for traits controlled by major genes or a few QTLs. Its efficiency decreases for complex polygenic traits and its application in moth bean is currently constrained by the limited availability of high-density markers and genomic resources.

Advanced backcross quantitative trait loci approach

The advanced backcross QTL (AB-QTL) approach integrates QTL mapping and introgression into a single breeding strategy, allowing simultaneous identification and transfer of beneficial alleles from wild relatives (61). In this approach, early backcross generations (e.g., BC₂ or BC₃) are used for phenotypic evaluation and genotyping to identify QTLs associated with desirable traits. This enables breeders to detect favourable alleles from wild species that may otherwise remain hidden due to the dominance of cultivated alleles. In moth bean, the AB-QTL approach has strong potential for identifying novel QTLs related to drought tolerance, heat stress adaptation and yield stability from wild species such as *V. trilobata* and *V. stipulacea* (27, 70). Unlike traditional QTL mapping populations, AB-QTL populations are directly useful in breeding programs, as they already contain a high proportion of the elite genetic background. This strategy is particularly valuable for improving complex traits, as it enables the capture and utilisation of multiple beneficial alleles from wild germplasm. However, it requires large population sizes, precise phenotyping and reliable marker systems for effective implementation.

Quantitative trait loci mapping and comparative genomics approaches

Quantitative trait loci mapping is essential for understanding complex adaptive traits. It helps identify genomic regions linked to drought tolerance, heat tolerance and nutrient efficiency in moth bean and its wild relatives. High-density linkage maps and bi-parental populations are commonly used for QTL mapping. These methods help identify loci associated with significant phenotypic variation. The detected loci serve as useful markers for marker-assisted and genomic selection. Next generation sequencing has improved QTL analysis. It enables a shift from low-resolution mapping to precise candidate gene identification. This allows better analysis of complex traits through genome-wide association studies and linkage disequilibrium analysis (71). In moth bean, genetic linkage maps have been developed using F₂ populations. These populations are derived from crosses between wild (TN 67) and cultivated accessions (ICPMO056). These studies have identified QTLs for domestication-related traits useful for crop improvement (9, 25). Comparative genomics further improves gene identification. It uses synteny and collinearity with closely related *Vigna* species, particularly mungbean and black gram and subsequently with model legumes like soybean and common bean. This helps transfer genomic knowledge and identify orthologous genes for stress tolerance (28).

Genomic selection represents an advanced breeding approach. It differs from marker-assisted selection by using genome-wide markers instead of a few loci. This improves selection efficiency for complex traits like yield under stress (69). Genomic selection models use both phenotypic and genotypic data. These models predict breeding values for untested lines, which accelerates genetic gain for traits controlled by many small-effect genes (72). However, the application of genomic selection in moth bean is still limited. This is due to the lack of high-density genotyping tools and large phenotypic datasets. Therefore, improved infrastructure for genotyping and phenotyping is required (72). Despite these advances in genomic tools and trait identification, the effective utilisation of wild genetic resources in moth bean breeding is often constrained by reproductive barriers. These barriers limit gene flow between cultivated and wild species, making it necessary to understand their nature before successful introgression can be achieved. Integrated pre-breeding and introgression breeding pipeline for climate-resilient moth bean development is illustrated in Fig. 3.

Reproductive barriers and constraints in moth bean wild relative hybridisation

The successful utilisation of wild relatives in moth bean improvement depends primarily on overcoming complex pre-zygotic and post-zygotic reproductive barriers that restrict gene flow between divergent gene pools, thereby

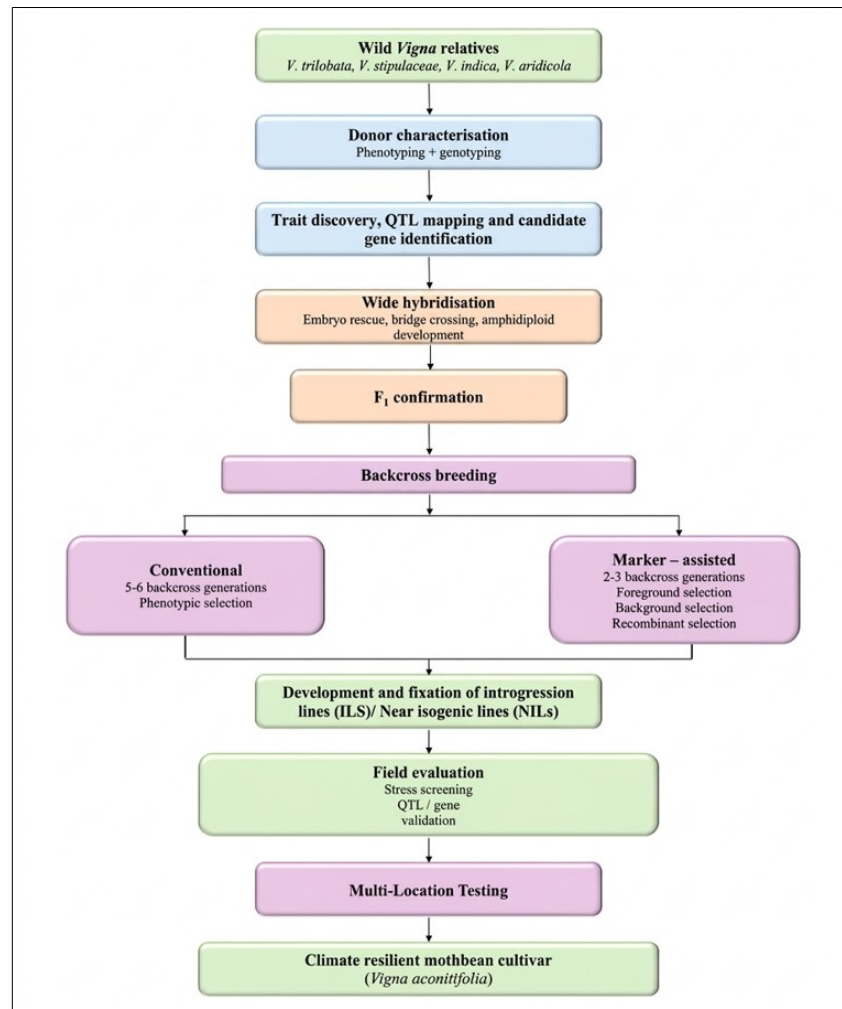


Fig. 3. Integrated pre-breeding and introgression breeding pipeline for climate-resilient moth bean development. The workflow illustrates the transfer of beneficial alleles from wild *Vigna* relatives into cultivated moth bean through wide hybridisation, backcross breeding, ntroggression line (IL)/near-isogenic line (NIL) development and field validation.

determining the success of interspecific hybridisation. Pre-zygotic barriers operate before fertilisation and commonly exhibit as pollen-pistil incompatibility. In such cases, pollen from wild *Vigna* species either fails to germinate on the stigma of cultivated *V. aconitifolia* or the pollen tube growth is arrested before reaching the ovule. This phenomenon, frequently observed in wide crosses within the genus *Vigna*, is primarily attributed to biochemical or structural incompatibilities between the maternal tissues and the incoming pollen, thereby preventing fertilisation despite successful pollination (22, 73). After fertilisation, post-zygotic barriers are often the most important limiting factor. These include hybrid inviability and sterility, resulting from genomic incompatibilities that disrupt normal embryo and endosperm development. A classic example is the interspecific cross between *V. aconitifolia* and *V. trilobata*, where hybrid development is adversely affected despite successful fertilisation. Wide crosses between these species frequently result in abnormal embryo development and reduced seed viability, indicating the presence of significant post-zygotic incompatibility. These effects are primarily caused by endosperm imbalance and disrupted genomic interactions between the parental

species, often leading to partial or complete failure of hybrid recovery (22, 37, 74).

In addition to hybrid inviability, hybrid sterility represents another major post-zygotic constraint in moth bean breeding. Although F_1 hybrids may appear morphologically normal, their reproductive potential is often severely affected due to meiotic irregularities and improper chromosomal pairing. This prevents the generation of viable segregating populations necessary for trait introgression (75, 76). Overall, these reproductive barriers operate at different stages of development, from the interaction of pollen and stigma to maturation of the embryo, making the introgression of useful traits from wild relatives into moth bean a challenging yet essential strategy for crop improvement (77).

Techniques for overcoming reproductive isolation

To overcome pre-zygotic barriers that restrict pollen tube growth in wide *Vigna* crosses, breeders use approaches such as compatible pollen mixtures, stigma treatments with growth regulators like gibberellic acid, boron and *in vitro* fertilisation to bypass stylar inhibition (78). When fertilisation is successful but seed

development fails, post-zygotic barriers become the major limitation. These are mainly caused by genomic incompatibility and endosperm failure. In such cases, *in vitro* embryo rescue serves as an important technique for recovering hybrid embryos. This technique involves excising immature embryos and culturing them on nutrient media to recover hybrids that would otherwise abort (77, 79). However, its success depends on early excision and proper nutrient supply, as embryos rely on external resources in the absence of endosperm support (80). Evidence from *Vigna* species indicates that embryo abortion often occurs at early stages due to endosperm collapse. For example, in crosses between cultivated cowpea and *Vigna vexillate* (L.) A.Rich., embryos arrest at the globular stage, which requires early intervention within a few days after pollination (81). Although growth regulators such as 2,4-D and 1-naphthaleneacetic acid (NAA) can delay pod abscission, they do not resolve the underlying endosperm dysfunction and thus fail to ensure viable seed development (81).

Apart from embryo rescue, other strategies are often more practical for overcoming post-zygotic barriers. Bridge crosses use an intermediate species to facilitate gene transfer between incompatible parents. Chromosome doubling through agents like colchicine or oryzalin restores fertility in sterile hybrids by enabling proper chromosomal pairing during meiosis (22, 82, 83). In addition, *in vivo* approaches such as the application of gibberellic acid and indole-3-acetic acid can delay flower abscission and pod retention. However, these methods only provide temporary support and do not correct genomic imbalance or endosperm failure, which remain the primary cause of hybrid lethality (74, 80). Therefore, while embryo rescue is an important supportive tool, it is not the only solution. Its effectiveness depends on the severity of endosperm dysfunction and the timing of intervention. In many cases, it must be integrated with other strategies such as bridge crossing and chromosome manipulation to successfully recover viable introgression lines in moth bean breeding programmes (84, 85). Advances in molecular breeding and precision genetic technologies such as genomic-assisted breeding or gene editing could further support the efficient incorporation of useful alleles from wild relatives.

Development and validation of introgression lines in moth bean

After overcoming hybridisation barriers and successfully introgressing desirable genomic regions from wild relatives, the next critical phase is the development and stabilisation of introgression lines (ILs). These lines consist of specific donor chromosomal segments that are incorporated into the genetic background of the cultivated parent, providing a reliable system to evaluate the expression of targeted traits such as drought tolerance, heat resilience and disease resistance under field conditions (61). In moth bean (*V. aconitifolia*), IL development is particularly important because most adaptive traits are quantitatively inherited and controlled

by multiple loci (QTLs mapping). After several backcrosses and selections, advanced generations (e.g., BC₂F₃, BC₃F₄) are selfed to achieve homozygosity, to ensure the stability of introgressed segments. These stabilised lines are then evaluated across diverse environments to assess trait expression, genotype-environment interactions and yield stability under stress conditions (64). Validation of these lines requires both phenotypic and molecular approaches. Key physiological traits such as enhanced root architecture, osmotic adjustment and delayed senescence are assessed under drought stress, while traits like pollen viability and reproductive stability are examined under heat stress. At the same time, molecular markers, including simple sequence repeats (SSRs), single-nucleotide polymorphisms (SNPs) and Kompetitive allele-specific polymerase chain reaction (KASP) markers that are linked to introgressed regions, are used to confirm the association between genotype and observed phenotype (68).

Beyond trait validation, ILs serve as powerful tools for fine mapping and gene discovery. A comparative analysis of lines with different donor segments enables pinpointing genomic regions linked to stress tolerance and identifying candidate genes. Additionally, IL populations serve as a stable breeding resource, facilitating the accumulation of various advantageous alleles into superior cultivars. However, well-characterised IL populations in moth bean remain rare, indicating a significant gap between introgression breeding efforts and improved varieties.

Socio-economic relevance and adoption of improved cultivars

Moth bean holds considerable importance in smallholder farming systems across arid and semi-arid regions of India. Its drought tolerance, low water requirement and suitability for rainfed cultivation make it particularly valuable under resource-limited conditions. Beyond grain production, the crop provides vegetables, fodder and livestock feed, contributing to household food and nutritional security. Western Rajasthan accounts for more than 94 % of national moth bean production, highlighting its importance to dryland livelihoods (86). Despite this significance, its market potential remains underutilised, although products such as dal, sprouts, flour and other processed foods offer opportunities for value addition (87). Seasonal concentration of market arrivals can, however, reduce prices during peak harvest periods and consequently affect farmer returns (88).

Wider adoption of improved cultivars is further influenced by the availability of quality seed, extension services and reliable market returns. Demonstrations of improved varieties and production practices have shown potential for increasing both yield and farm income (86). Strengthening seed delivery systems, processing facilities, market linkages and farmer-oriented extension could therefore improve the adoption and profitability of improved cultivars. Accordingly, future breeding



programmes should consider farmer-preferred traits, market demand and end-use quality alongside drought, heat and disease resistance to ensure that improved moth bean cultivars are both agronomically superior and economically attractive to farmers.

Policy and institutional support for moth bean genetic improvement

Effective utilisation of moth bean genetic diversity requires coordinated support for germplasm conservation, breeding and resource exchange. In India, ICAR-National Bureau of Plant Genetic Resources (NBPGR) serves as the major national repository for plant genetic resources and holds more than 3400 moth bean accessions, while ICAR-Indian Institute of Pulses Research (IIPR) includes moth bean within its crop-improvement mandate. Its activities include germplasm collection, conservation, characterisation and mutation breeding for generating useful variability. The ICAR-IIPR Bikaner centre also undertakes moth bean breeding, germplasm evaluation and screening for drought, heat and pest resistance (89). At the national level, the All India Coordinated Research Project (AICRP) on kharif pulses coordinates research on moth bean across different centres, supporting genetic improvement, germplasm utilisation, seed production and technology dissemination. Recent development of CAZRI Moth-4 and CAZRI Moth-5 further demonstrates ongoing efforts to develop high-yielding, short-duration cultivars adapted to rainfed environments (90). Strengthening collaboration among genebanks, breeding institutions and agricultural universities can therefore facilitate the transfer of conserved diversity into climate-resilient breeding programmes.

The utilisation and exchange of wild genetic resources must also consider intellectual property and access-and-benefit-sharing requirements. In India, access to biological resources and associated traditional knowledge is governed by the Biological Diversity Act and related regulations, with benefit-sharing mechanisms administered through the National Biodiversity Authority. Internationally, the International Treaty on Plant Genetic Resources for Food and Agriculture provides a framework for facilitated access to relevant plant genetic resources and equitable benefit sharing (4). For moth bean, proper documentation of germplasm origin, appropriate material-transfer arrangements and compliance with applicable access requirements are important when wild relatives are used in breeding. Such measures can promote responsible germplasm exchange while supporting equitable recognition of genetic-resource contributions.

Climate change scenarios and implications for moth bean production

Moth bean is predominantly cultivated in the arid and semi-arid regions of northwestern India, particularly Rajasthan and Gujarat. These regions are projected to experience increasing temperatures, rainfall variability and heat stress under future climate scenarios (9, 91). Such changes may increase evaporative demand and

reduce the stability of crop production, despite moth bean's inherent drought and heat tolerance. Climate change may also alter the suitability of existing production environments by affecting temperature, rainfall and soil-moisture availability. This highlights the need for breeding short-duration, drought- and heat-resilient cultivars with stable performance across environments. Future breeding programmes should therefore integrate climate projections with multi-environment testing to identify and deploy traits suited to emerging production conditions.

Regulatory, biosafety and public acceptance considerations

In India, genome-edited crops are regulated within the national biosafety framework established under the Environment (Protection) Act, 1986 and the Rules, 1989. The Guidelines for the Safety Assessment of Genome Edited Plants (2022) provide specific guidance for genome-edited crops, while SDN-1 and SDN-2 plants without exogenous DNA are exempt from specified provisions of the 1989 Rules, but SDN-3 products remain subject to the established biosafety assessment framework (92). For introgressed moth bean lines, biosafety evaluation should consider genetic stability, donor-segment characterisation, linkage drag, gene flow, weediness, effects on non-target organisms and nutritional or anti-nutritional composition. Molecular characterisation and multi-location evaluation will therefore be important before their wider deployment. Public acceptance will also influence the adoption of improved moth bean cultivars. Perceptions of safety, breeding methods, ownership and potential benefits may shape farmer and consumer responses, particularly when advanced techniques are involved. Transparent communication of the breeding process, safety assessments and expected benefits, such as drought tolerance, yield stability and reduced input requirements, can help build confidence. Participatory evaluation involving farmers, consumers and other stakeholders can further strengthen trust and support the responsible adoption of improved moth bean lines.

Challenges and limitations of introgression breeding in moth bean

Despite its potential, introgression breeding in moth bean is constrained by several key challenges. Reproductive barriers during wide hybridisation, including pre- and post-zygotic incompatibilities, often result in hybrid sterility and reduced fertility, limiting effective gene transfer from wild relatives (78). Selecting compatible parents and reciprocal crosses can improve hybridisation success (15). Embryo rescue can recover hybrid embryos that fail during development.

Repeated backcrossing can subsequently restore fertility and elite genetic backgrounds. Linkage drag further complicates improvement, as undesirable traits are frequently co-introduced with beneficial alleles, making it difficult to recover elite genotypes even after repeated backcrossing (78). Marker-assisted backcrossing, together with foreground and background



selection, can facilitate the recovery of elite genotypes while reducing unwanted donor segments. Subsequent recombinant selection can further minimise the remaining linked undesirable regions (25, 56). In addition, important adaptive traits such as drought and heat tolerance are polygenic, governed by multiple loci studied under QTLs mapping are highly influenced by environmental factors (24). Multi-environment phenotyping, QTL validation and integration of GWAS with genomic selection can improve selection accuracy. Although moth bean remains comparatively under-resourced genomically, genotyping-by-sequencing (GBS) analysis of 428 accessions identified 9078 high-quality SNPs, demonstrating progress towards genome-enabled breeding (23). Further validation of marker-trait associations and development of reliable genomic resources are therefore needed. In addition, limited characterisation of wild germplasm and labour-intensive phenotyping can hinder donor identification; systematic germplasm characterisation, core collections and standardised multi-environment screening can improve the utilisation of available diversity (9).

Economic constraints

The adoption of genomic approaches in moth bean may be constrained by the costs associated with genotyping, sequencing, bioinformatics and computational infrastructure. These requirements can be particularly challenging for an underutilised crop, where breeding programmes often operate with limited resources. However, the use of cost-effective genotyping platforms such as GBS, together with shared sequencing and bioinformatics facilities, can reduce the overall investment. Moreover, genomic selection can improve cost efficiency when applied to large breeding populations or traits that are expensive and labour-intensive to phenotype (93). Therefore, integrating targeted genomic approaches with conventional phenotypic selection could provide a practical and economically feasible strategy for accelerating moth bean improvement.

Future perspectives

Despite advances in related legume crops, there are still notable gaps remain in moth bean research, especially in the effective utilisation of wild genetic resources and in decoding the mechanisms underlying climate resilience. Future efforts, therefore, should focus on translating existing genetic potential into practical breeding outcomes through the integration of advanced tools and coordinated research efforts. Priority should be given to implementing high-resolution mapping approaches, including QTL mapping and genome-wide association studies, in well-structured introgression populations to identify genomic regions governing stress tolerance precisely. Next-generation genome editing technologies like CRISPR-Cas, base editing and prime editing offer a promising way to directly incorporate useful alleles into elite cultivars. This speeds up genetic improvement and reduces the need for prolonged backcrossing cycles (94, 95). In addition, integrating

high throughput phenomics with bioinformatics and predictive modelling can improve the accuracy of trait evaluation across diverse environments and facilitate the selection of complex traits (96, 97).

Moreover, the integration of genomic and phenotypic data through centralised databases and digital gene banks will facilitate more informed breeding decisions. Strengthening collaborative networks and standardising data collection protocols will enable large-scale analyses and improve the predictive precision of genomic selection across diverse environments (97, 98). The integration of precision breeding, functional genomics and data-driven methodologies will be essential for expediting the advancement of climate-resilient moth bean cultivars and improving genetic gains in this underutilised crop (24, 99).

4. Conclusion

The utilisation of wild relatives plays a critical role in enhancing climate resilience in moth bean (*Vigna aconitifolia*), while addressing the gap between its underexplored genetic diversity and current breeding progress. Although moth bean is naturally adapted to arid conditions, its improvement is constrained by a narrow genetic base and limited genomic resources. In this context, wild *Vigna* species serve as an essential reservoir of adaptive traits needed to overcome yield limitations and sustain productivity under changing climates. Effective utilisation of these resources requires a shift from conventional breeding to integrative genomics-assisted approaches that address reproductive barriers and complex trait inheritance. The combined use of marker-assisted selection and genomic selection, along with techniques like embryo rescue and bridge crossing, can improve the efficiency of introgression from wild species. Future research should focus on systematically characterising wild gene pools and validating marker trait associations. Multi-environment evaluation of introgressed materials will be essential to confirm trait stability and breeding value. Greater emphasis on high-throughput phenotyping and cost-effective genotyping can strengthen selection for drought, heat and yield-related traits. Ultimately, sustainable improvement of moth bean will depend on an integrated breeding strategy incorporating pre-breeding, high-throughput genotyping and systematic utilisations of wild gene pools to unlock hidden genetic variation and achieve stable yields under diverse environmental stress conditions.

Acknowledgements

The authors are grateful to V. O. Chidambaranar Agricultural College and Research Institute, Killikulam, Tamil Nadu, India and Rice Research Station, Ambasamudram, Tamil Nadu, India for providing the necessary resources and facilities to conduct this study.



Authors' contributions

SKS prepared the initial draft and contributed to writing, review and editing. SS supervised the study and critically revised the manuscript. SJH contributed to visualisation and investigation. JS conceptualised the study and AKP contributed to the final improvement of the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used Grammarly, ChatGPT and Claude AI to improve the language and readability. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

References

- Abrol IP, Sangar S. Sustaining Indian agriculture-conservation agriculture the way forward. *Curr Sci*. 2006;1020–5.
- Cummings RW, RS Paroda: Reorienting Indian agriculture: challenges and opportunities. *Food Secur*. 2019;11(4):985–6. <https://doi.org/10.1007/s12571-019-00955-6>
- Birthal PS, Srivastava SK, Saxena R, Godara S, Chand P, Kishore P, et al. Indian Agriculture to 2047: Reshaping Policies for Sustainable Development. New Delhi: ICAR-National Institute of Agricultural Economics and Policy Research; 2025.
- Food and Agriculture Organization. FAOSTAT production database: Crops and livestock products. Rome: FAO; 2025.
- Gruère G, Giuliani A, Smale M. Marketing underutilized plant species for the benefit of the poor: a conceptual framework. *Intl Food Policy Res Inst*. 2006. <https://doi.org/10.2139/ssrn.916572>
- van Zonneveld M, Rakha M, Tan SY, Chou YY, Chang CH, Yen JY, et al. Mapping patterns of abiotic and biotic stress resilience uncovers conservation gaps and breeding potential of *Vigna* wild relatives. *Sci Rep*. 2020;10(1):2111. <https://doi.org/10.1038/s41598-020-58646-8>
- Heuzé V, Tran G, Lebas F. Sainfoin Moth bean (*Vigna aconitifolia*). Feedipedia, a programme by INRAE, CIRAD, AFZ and FAO. 2020.
- Saravanan M, Ignacimuthu S. Hypcholesterolemic effect of Indian medicinal plants—a review. *Med Chem*. 2015;5(1):040–9. <https://doi.org/10.4172/2161-0444.1000241>
- Kanishka RC, Gayacharan C, Basavaraja T, Chandora R, Rana JC. Moth bean (*Vigna aconitifolia*): a minor legume with major potential to address global agricultural challenges. *Front Plant Sci*. 2023;14. <https://doi.org/10.3389/fpls.2023.1179547>
- Singh AK, Singh CK, Sinha S, Gayacharan. Genetics and Omics Approaches for Moth Bean Improvement. In: Legumes: Genetics and Genomics. Singapore: Springer Nature Singapore; 2026. p. 1–25. https://doi.org/10.1007/978-981-97-7538-5_24-1
- Rajpal VR, Singh A, Kathpalia R, Thakur RK, Khan MK, Pandey A, et al. The prospects of gene introgression from crop wild relatives into cultivated lentil for climate change mitigation. *Front Plant Sci*. 2023;14:1127239. <https://doi.org/10.3389/fpls.2023.1127239>
- Verdcourt B. Studies in the Leguminosae-Papilionoideae for the 'Flora of Tropical East Africa': IV. *Kew Bull*. 1970;507–69. <https://doi.org/10.2307/4102859>
- Takahashi Y, Somta P, Muto C, Iseki K, Naito K, Pandiyan M, et al. Novel genetic resources in the genus *Vigna* unveiled from gene bank accessions. *PLoS One*. 2016;11(1):e0147568. <https://doi.org/10.1371/journal.pone.0147568>
- Suranjika S, Pradhan S, Kalia RK, Dey N. De novo assembly of the whole genome of Moth bean (*Vigna aconitifolia*), an underutilized *Vigna* species of India. *bioRxiv*. 2023. <https://doi.org/10.1101/2023.05.18.540937>
- Rani J, Dhull SB, Kinabo J, Kidwai MK, Sangwan A. A narrative review on nutritional and health benefits of underutilized summer crop to address agriculture challenges: Moth bean (*Vigna aconitifolia* L.). *Legume Sci*. 2023;5(4):e204. <https://doi.org/10.1002/leg3.204>
- Yadav AK, Singh CK, Wankhede DP, Kalia RK, Pradhan S, Ujjainwal S, et al. Combined genome-wide association study and expression analysis unravels candidate genes associated with seed weight in moth bean [*Vigna aconitifolia* (Jacq.) Marechal]. *J Plant Growth Regul*. 2025;44(5):1973–86. <https://doi.org/10.1007/s00344-024-11517-2>
- Candolle A. Origin of cultivated plants. *Litres*; 2021. <https://doi.org/10.5962/bhl.title.20259>
- Maréchal R. Taxonomic study of a complex group of species of the genera *Phaseolus* and *Vigna* (Papilionaceae) on the basis of morphological and pollen data, processed by computer analysis. *Boissiera*. 1978;28:1–273.
- Tomooka N, Kaga A, Isemura T, Vaughan D. *Vigna*. In: Wild crop relatives: genomic and breeding resources. Legume crops and forages. Berlin, Heidelberg: Springer Berlin Heidelberg; 2010. p. 291–311. https://doi.org/10.1007/978-3-642-14387-8_15
- Shah TI, Rai AP, Ma A. Relationship of phosphorus fractions with soil properties in mothbean growing acid soils of North Western Indian Himalayas. *Commun Soil Sci Plant Anal*. 2019;50(9):1192–8. <https://doi.org/10.1080/00103624.2019.1604730>
- Choudhary KB, Sharma R, Solanki RK, Mahla HR, Jadon KS, Choudhary M, et al. Genetic relatedness in elite cultivars of moth bean using morpho-agronomic and molecular markers. *Legume Res*. 2024;47(3). <https://doi.org/10.18805/LRF-774>



22. Bhanu AN, Singh MN, Srivastava K. Efficient hybridization procedure for better pod setting in inter-specific crosses involving *Vigna* species. *Adv Plants Agric Res.* 2018;8:101–5. <https://doi.org/10.15406/apar.2018.08.00298>
23. Yadav AK, Singh CK, Kalia RK, Mittal S, Wankhede DP, Kakani RK, et al. Genetic diversity, population structure and genome-wide association study for the flowering trait in a diverse panel of 428 moth bean (*Vigna aconitifolia*) accessions using genotyping by sequencing. *BMC Plant Biol.* 2023;23(1):228. <https://doi.org/10.1186/s12870-023-04215-w>
24. Singh G, Gudi S, Amandeep, Upadhyay P, Shekhawat PK, Nayak G, et al. Unlocking the hidden variation from wild repository for accelerating genetic gain in legumes. *Front Plant Sci.* 2022;13:1035878. <https://doi.org/10.3389/fpls.2022.1035878>
25. Yundaeng C, Somta P, Amkul K, Kongjaimun A, Kaga A, Tomooka N. Construction of genetic linkage map and genome dissection of domestication-related traits of moth bean (*Vigna aconitifolia*), a legume crop of arid areas. *Mol Genet Genom.* 2019;294(3):621–35. <https://doi.org/10.1007/s00438-019-01536-0>
26. Dwivedi SL, Chapman MA, A645bberton MT, Akpojotor UL, Ortiz R. Exploiting genetic and genomic resources to enhance productivity and abiotic stress adaptation of underutilized pulses. *Front Genet.* 2023;14:1193780. <https://doi.org/10.3389/fgene.2023.1193780>
27. Pandey MK, Roorkiwal M, Singh VK, Ramalingam A, Kudapa H, Thudi M, et al. Emerging genomic tools for legume breeding: current status and future prospects. *Front Plant Sci.* 2016;7:455. <https://doi.org/10.3389/fpls.2016.00455>
28. Bhimireddy S, Kumar AN, Vemireddy LN, Reddy CK, Akkareddy S. Possibility for exploitation and identification of rice yield and seed quality orthologs in peanut (*Arachis hypogaea* L.). *Legume Res.* 2026;49(2):292–8. <https://doi.org/10.18805/LR-5309>
29. Halladakeri P, Gudi S, Akhtar S, Singh G, Saini DK, Hilli HJ, et al. Meta-analysis of the quantitative trait loci associated with agronomic traits, fertility restoration, disease resistance and seed quality traits in pigeonpea (*Cajanus cajan* L.). *Plant Genome.* 2023;16(3):e20342. <https://doi.org/10.1002/tpg2.20342>
30. Roorkiwal M, Bharadwaj C, Barmukh R, Dixit GP, Thudi M, Gaur PM, et al. Integrating genomics for chickpea improvement: achievements and opportunities. *Theor Appl Genet.* 2020;133(5):1703–20. <https://doi.org/10.1007/s00122-020-03584-2>
31. Varshney RK, Close TJ, Singh NK, Hoisington DA, Cook DR. Orphan legume crops enter the genomics era! *Curr Opin Plant Biol.* 2009;12(2):202–10. <https://doi.org/10.1016/j.pbi.2008.12.004>
32. Salgotra RK, Stewart CN Jr. Genetic augmentation of legume crops using genomic resources and genotyping platforms for nutritional food security. *Plants.* 2022;11(14):1866. <https://doi.org/10.3390/plants11141866>
33. Singh B, Bohra A, Mishra S, Joshi R, Pandey S. Embracing new-generation 'omics' tools to improve drought tolerance in cereal and food-legume crops. *Biol Plant.* 2015;59(3):413–28. <https://doi.org/10.1007/s10535-015-0515-0>
34. Bohra A, Tiwari A, Kaur P, Ganie SA, Raza A, Roorkiwal M, et al. The key to the future lies in the past: insights from grain legume domestication and improvement should inform future breeding strategies. *Plant Cell Physiol.* 2022;63(11):1554–72. <https://doi.org/10.1093/pcp/pcac086>
35. Kaga A, Tomooka N, Egawa Y, Hosaka K, Kamijima O. Species relationships in the subgenus *Ceratotropis* (genus *Vigna*) as revealed by RAPD analysis. *Euphytica.* 1996;88(1):17–24. <https://doi.org/10.1007/BF00029261>
36. Sampson HC. Crop plants of the British Empire. *Nature.* 1936;137:544–5. <https://doi.org/10.1038/137544b0>
37. Dana S. Genomic relationship in the genus *Vigna* and its implications in the breeding programme. In: *Breeding methods for the improvement of pulse crops.* 1980. p. 357–67.
38. Biswas MR, Dana S. *Phaseolus aconitifolius* × *Phaseolus trilobus*. *Indian J Genet Plant Breed.* 1976;36(1):125–31.
39. Chankaew S, Isemura T, Naito K, Ogiso-Tanaka E, Tomooka N, Somta P, et al. QTL mapping for salt tolerance and domestication-related traits in *Vigna marina* subsp. *oblonga*, a halophytic species. *Theor Appl Genet.* 2014;127(3):691–702. <https://doi.org/10.1007/s00122-013-2251-1>
40. Bisht IS, Bhat KV, Lakhanpaul S, Latha M, Jayan PK, Biswas BK, et al. Diversity and genetic resources of wild *Vigna* species in India. *Genet Resour Crop Evol.* 2005;52(1):53–68. <https://doi.org/10.1007/s10722-005-0286-0>
41. Kana Hau D, Nulik J, Field SP, Kieft J, Ella A, Bahar S, et al. Forty years' trajectory of forage legume species introduction, adaptation, cultivation and their usage strategies in livestock feeding and farming systems in the semi-arid region of eastern Indonesia: a review. *Asian J Agric Biol.* 2025. <https://doi.org/10.2139/ssrn.4934793>
42. Maxted N, Ford-Lloyd BV, Jury S, Kell S, Scholten M. Towards a definition of a crop wild relative. *Biodivers Conserv.* 2006;15(8):2673–85. <https://doi.org/10.1007/s10531-005-5409-6>
43. Harlan JR, de Wet JM. Toward a rational classification of cultivated plants. *Taxon.* 1971;20(4):509–17. <https://doi.org/10.2307/1218252>
44. Tomooka N, Vaughan D, Moss H, Maxted N. The Asian *Vigna*: genus *Vigna* subgenus *Ceratotropis* genetic resources. Springer; 2012. https://doi.org/10.1007/978-94-010-0314-8_3
45. Zhou C, Wang H, Zhu X, Li Y, Zhang B, Tadege M, et al. Functional genomics: from soybean to legume. *Int J Mol Sci.* 2025;26(13):6323. <https://doi.org/10.3390/ijms26136323>
46. Tomooka N, Naito K, Kaga A, Sakai H, Isemura T, Ogiso-Tanaka E, et al. Evolution, domestication and neo-domestication of the genus *Vigna*. *Plant Genet Resour.* 2014;12(S1):S168–71. <https://doi.org/10.1017/S1479262114000483>
47. Kumar J, Choudhary AK, Gupta DS, Kumar S. Towards exploitation of adaptive traits for climate-resilient smart pulses. *Int J Mol Sci.* 2019;20(12):2971. <https://doi.org/10.3390/ijms20122971>
48. Nagaraj NC, Muniyappa V, Satyan BA. Resistance source for mung bean yellow mosaic virus. In: *Proceedings of the National Seminar on Disease Resistance in Crop Plants.* 1981.
49. Takahashi Y, Sakai H, Yoshitsu Y, Muto C, Anai T, Pandiyan M, et al. Domesticating *Vigna stipulacea*: a potential legume crop with broad resistance to biotic stresses. *Front Plant Sci.* 2019;10:1607. <https://doi.org/10.3389/fpls.2019.01607>



50. Dwivedi SL, Scheben A, Edwards D, Spillane C, Ortiz R. Assessing and exploiting functional diversity in germplasm pools to enhance abiotic stress adaptation and yield in cereals and food legumes. *Front Plant Sci.* 2017;8:1461. <https://doi.org/10.3389/fpls.2017.01461>
51. Kondo N, Tomooka N. New sources of resistance to *Cadophora gregata* f. sp. *Adzukicola* and *Fusarium oxysporum* f. sp. *Adzukicola* in *Vigna* spp. *Plant Dis.* 2012;96(4):562–8. <https://doi.org/10.1094/PDIS-06-11-0463>
52. Chadburn H. *Vigna khandalensis*. The IUCN Red List of Threatened Species. 2012:e.T19892969A20163711.
53. Raghavan SR. On the nomenclature of *Vigna grandis* (Dalz. & Gibs.) Verdc. *Curr Sci.* 1972;41:429.
54. Umdale SD, Chavan JJ, Ahire ML, Kshirsagar PR, Gaikwad NB, Bhat KV. *Vigna khandalensis* (Santapau) Raghavan et Wadhwa: a promising underutilized, wild, endemic legume of the Northern Western Ghats, India. *Genet Resour Crop Evol.* 2018;65(6):1795–807. <https://doi.org/10.1007/s10722-018-0657-y>
55. Shamurailatpam A, Wahlang DR, Madhavan L, Yadav SR, Bhat KV, Rao SR. Further observations on chromosome diversity analysis in wild species of *Vigna* from India. *Nucleus.* 2015;58(3):225–30. doi:10.1007/s13237-016-0157-4. <https://doi.org/10.1007/s13237-016-0157-4>
56. Somta P, Jomsangawong A, Yundaeng C, Yuan X, Chen J, Tomooka N, et al. Genetic dissection of azuki bean weevil (*Callosobruchus chinensis* L.) resistance in moth bean (*Vigna aconitifolia* [Jacq.] Maréchal). *Genes.* 2018;9(11):555. <https://doi.org/10.3390/genes9110555>
57. Gamage SI, Kaewwongwal A, Laosatit K, Yimram T, Lin Y, Chen X, et al. Tandemly duplicated genes encoding polygalacturonase inhibitors are associated with bruchid (*Callosobruchus chinensis*) resistance in moth bean (*Vigna aconitifolia*). *Plant Sci.* 2022;323:111402. <https://doi.org/10.1016/j.plantsci.2022.111402>
58. Singh K, Shekhawat N, Singh OV, Choudhary M, Ram D. Identification for sources of resistance to biotic stresses in mothbean [*Vigna aconitifolia* (Jacq.) Marechal] germplasm. *Int J Curr Microbiol Appl Sci.* 2020;9(5):1243–9. <https://doi.org/10.20546/ijcmas.2020.905.138>
59. Meena MK, Dogra I, Sudarsan Y, Sharma AK, Singh D, Sharma V, et al. Identification and characterization of CAT1 gene during drought stress in moth bean [*Vigna aconitifolia* (Jacq.) Marechal]. *J Agric Ecol.* 2022;14:164–72. <https://doi.org/10.58628/JAE-2214-224>
60. Iseki K, Takahashi Y, Muto C, Naito K, Tomooka N. Diversity of drought tolerance in the genus *Vigna*. *Front Plant Sci.* 2018;9:729. <https://doi.org/10.3389/fpls.2018.00729>
61. Tanksley SD, Nelson JC. Advanced backcross QTL analysis: a method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. *Theor Appl Genet.* 1996;92(2):191–203. <https://doi.org/10.1007/BF00223376>
62. Hospital F. Selection in backcross programmes. *Philos Trans R Soc Lond B Biol Sci.* 2005;360(1459):1503–11. <https://doi.org/10.1098/rstb.2005.1670>
63. Anderson E, Hubricht L. Hybridization in *Tradescantia*. III. The evidence for introgressive hybridization. *Am J Bot.* 1938;396–402. <https://doi.org/10.1002/j.1537-2197.1938.tb09237.x>
64. Singh P, Pandey B, Pratap A, Gyaneshwari U, Nair RM, Mishra AK, et al. Genetic and genomics resources of cross-species *Vigna* gene pools for improving biotic stress resistance in mungbean (*Vigna radiata* L. Wilczek). *Agronomy.* 2022;12(12):3000. <https://doi.org/10.3390/agronomy12123000>
65. Biodiversity International, GIPB/FAO. 2008.
66. Sagar KR, Srinivasulu B, Vamsi B. The impact of pre-breeding on vegetable crop improvement: a review. *J Exp Agric Int.* 2024;46(8):268–82. <https://doi.org/10.9734/jeai/2024/v46i82704>
67. Sharma S, Upadhyaya HD, Varshney RK, Gowda CL. Pre-breeding for diversification of primary gene pool and genetic enhancement of grain legumes. *Front Plant Sci.* 2013;4:309. <https://doi.org/10.3389/fpls.2013.00309>
68. Collard BC, Mackill DJ. Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. *Philos Trans R Soc Lond B Biol Sci.* 2008;363(1491):557–72. <https://doi.org/10.1098/rstb.2007.2170>
69. Varshney RK, Ribaut JM, Buckler ES, Tuberosa R, Rafalski JA, Langridge P. Can genomics boost productivity of orphan crops? *Nat Biotechnol.* 2012;30(12):1172–6. <https://doi.org/10.1038/nbt.2440>
70. Bohra A, Jha UC, Kishor PK, Pandey S, Singh NP. Genomics and molecular breeding in lesser explored pulse crops: current trends and future opportunities. *Biotechnol Adv.* 2014;32(8):1410–28. <https://doi.org/10.1016/j.biotechadv.2014.09.001>
71. Ni Z, Moeiniazade S, Kusmec A, Hu G, Wang L, Schnable PS. New insights into trait introgression with the look-ahead intercrossing strategy. *G3 (Bethesda).* 2023;13(4):jkad042. <https://doi.org/10.1093/g3journal/jkad042>
72. Prabhu KR, Kumar A, Yumkhaibam RS, Janeja HS, Bal K, Talekar N. A review on conventional and modern breeding approaches for developing climate resilient crop varieties. *J Appl Nat Sci.* 2023;15(3):987. <https://doi.org/10.31018/jans.v15i3.4653>
73. Keneni G, Ahmed S. Genetic options for combating biotic stresses in cool-season food legumes. *Indian J Genet Plant Breed.* 2016;76(4):437–50. <https://doi.org/10.5958/0975-6906.2016.00062.6>
74. Sharma S, Mittal RK, Chaudhary HK, Sood VK. Introgression of disease resistance in urdbean (*Vigna mungo*) by involving its related species. *Indian J Agric Sci.* 2022;92:1348–52. <https://doi.org/10.56093/ijas.v92i11.124619>
75. Tondonba SP, Khanna VK, Tejaswini VU. Crossability studies and genetic diversity analysis in blackgram (*Vigna mungo* L. Hepper) using molecular markers. *Agrotechnology.* 2018;2(7):179. <https://doi.org/10.4172/2168-9881.1000179>
76. Mahla HR, Sharma R. An easy method of artificial hybridization in two arid legumes, guar (*Cyamopsis tetragonoloba* Taub.) and moth bean [*Vigna aconitifolia* (Jacq.) Marechal]. *Indian J Genet Plant Breed.* 2022;82(1):109–12. <https://doi.org/10.31742/IJGPB.82.1.16>
77. Anushma P, Dhanyasree K, Rafeekher M. Wide hybridization for fruit crop improvement: a review. *Int J Chem Stud.* 2021;9:769–73. <https://doi.org/10.22271/chemi.2021.v9.i1k.11317>
78. Prohens J, Gramazio P, Plazas M, Dempewolf H, Kilian B, Díez MJ, et al. Introgressomics: a new approach for using crop wild relatives in breeding for adaptation to climate change. *Euphytica.* 2017;213(7):158. <https://doi.org/10.1007/s10681-017-1938-9>



79. Kumari P, Thaneshwari R. Embryo rescue in horticultural crops. *Int J Curr Microbiol Appl Sci*. 2018;7(6):3350–8. <https://doi.org/10.20546/ijcmas.2018.706.393>
80. He H, Shiragaki K, Tezuka T. Understanding and overcoming hybrid lethality in seed and seedling stages as barriers to hybridization and gene flow. *Front Plant Sci*. 2023;14:1219417. <https://doi.org/10.3389/fpls.2023.1219417>
81. Boukar O, Abberton M, Oyatomi O, Togola A, Tripathi L, Fatokun C. Introgression breeding in cowpea [*Vigna unguiculata* (L.) Walp.]. *Front Plant Sci*. 2020;11:567425. <https://doi.org/10.3389/fpls.2020.567425>
82. Huyghe C. *In vitro* techniques in grain legume crops. *Agronomie*. 1990;10(1):29–49. <https://doi.org/10.1051/agro:19900105>
83. Warchoła M, Czyczyło-Mysza I, Marcińska I, Dziurka K, Noga A, Skrzypek E. The effect of genotype, media composition, pH and sugar concentrations on oat (*Avena sativa* L.) doubled haploid production through oat × maize crosses. *Acta Physiol Plant*. 2018;40(5):93. <https://doi.org/10.1007/s11738-018-2669-9>
84. Encina CL, Regalado JJ. Aspects of *in vitro* plant tissue culture and breeding of asparagus: a review. *Horticulturae*. 2022;8(5):439. <https://doi.org/10.3390/horticulturae8050439>
85. Zhang F, Hua L, Fei J, Wang F, Liao Y, Fang W, et al. Chromosome doubling to overcome the chrysanthemum cross barrier based on insight from transcriptomic and proteomic analyses. *BMC Genomics*. 2016;17(1):585. <https://doi.org/10.1186/s12864-016-2939-0>
86. Meena MS, Mishra JP, Meena HN. Popularization of mothbean cultivation. *Indian Farming*. 2024;74(3):21–5.
87. Kumawat S. An economics of moth bean processing in Nagaur District of Rajasthan. *Ann Arid Zone*. 2016;55(1–2):59–61. <https://doi.org/10.56093/aaz.v55i1-2.62952>
88. Kumawat S, Singh IP. Trend analysis in market arrivals and prices of moth bean in Rajasthan. *Indian J Econ Dev*. 2015;11(4):843–50. <https://doi.org/10.5958/2322-0430.2015.00092.X>
89. Mahla HR, Choudhary KB, Sharma R, Singh K. Variety CAZRI Moth-4. *Indian J Genet Plant Breed*. 2024;84(2):315–6.
90. Indian Council of Agricultural Research. ICAR annual report 2024–25. New Delhi: ICAR; 2025.
91. Center for Study of Science, Technology and Policy (CSTEP). Climate change projections and vulnerability assessment for Rajasthan. Bengaluru: CSTEP; 2024.
92. Sharma N, Thakur K, Zinta R, Mangal V, Dalamu, Tiwari JK, et al. Genome editing research initiatives and regulatory landscape of genome edited crops in India. *Transgenic Res*. 2025;34(1):13. <https://doi.org/10.1007/s11248-025-00432-1>
93. Annicchiarico P, Nazzicari N, Wei Y, Pecetti L, Brummer EC. Genotyping-by-sequencing and its exploitation for forage and cool-season grain legume breeding. *Front Plant Sci*. 2017;8:679. <https://doi.org/10.3389/fpls.2017.00679>
94. Razzaq A, Wani SH, Saleem F, Yu M, Zhou M, Shabala S. Rewilding crops for climate resilience: economic analysis and de novo domestication strategies. *J Exp Bot*. 2021;72(18):6123–39. <https://doi.org/10.1093/jxb/erab276>
95. Chavhan RL, Jaybhaye SG, Hinge VR, Deshmukh AS, Shaikh US, Jadhav PK, et al. Emerging applications of gene editing technologies for the development of climate-resilient crops. *Front Genome Ed*. 2025;7:1524767. <https://doi.org/10.3389/fgeed.2025.1524767>
96. Khan T, Shah L, Khan S, Wani OA, Sheikh ZN, Afroza B, et al. Comprehensive review of multiomics applications and remediation of plant heavy metal toxicity. *Stress Biol*. 2025;5(1):58. <https://doi.org/10.1007/s44154-025-00233-w>
97. Varshney RK, Kudapa H, Pazhamala L, Chitkineni A, Thudi M, Bohra A, et al. Translational genomics in agriculture: some examples in grain legumes. *Crit Rev Plant Sci*. 2015;34(1–3):169–94. <https://doi.org/10.1080/07352689.2014.897909>
98. Popoola JO, Aworunse OS, Ojuederie OB, Adewale BD, Ajani OC, Oyatomi OA, et al. The exploitation of orphan legumes for food, income and nutrition security in Sub-Saharan Africa. *Front Plant Sci*. 2022;13:782140. <https://doi.org/10.3389/fpls.2022.782140>
99. Baloglu MC, Celik Altunoglu Y, Baloglu P, Yildiz AB, Türkölmez N, Özden Çiftçi Y. Gene-editing technologies and applications in legumes: progress, evolution and future prospects. *Front Genet*. 2022;13:859437. <https://doi.org/10.3389/fgene.2022.859437>

Additional information

Peer review: Publisher thanks the Sectional Editor and anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information: Available at https://horizonpublishing.com/journals/index.php/PST/open_access_policy.

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: See https://horizonpublishing.com/journals/index.php/PST/indexing_abstracting.

Copyright: © The Author(s). This is an open-access article distributed under the Creative Commons Attribution License CC BY 4.0.

Publisher information: Plant Science Today is published by Horizon e-Publishing Group with support from Empirion Publishers Private Limited, Thiruvananthapuram, India.

