

Towards climate-resilient phalsa (*Grewia subinaequalis* DC.): advances in genetics and breeding

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Summary

Grewia subinaequalis DC. (Phalsa) is a hardy, nutrient-dense, and economically valuable fruit crop native to Southeast Asia, yet it remains underexploited due to persistent agronomic and post-harvest constraints. This paper presents a comprehensive, evidence-based assessment of the current status and future directions in Phalsa breeding and genetics, designed for an academic readership. It critically evaluates the available genetic resources, underscoring the considerable but underutilized diversity within Indian germplasm, which has been characterized through both morpho-agronomic descriptors and molecular markers such as SSRs. An analysis of breeding approaches indicates that progress has historically relied on conventional selection, yielding only incremental improvements, while advanced methods like hybridization face limitations arising from the species' floral biology. The discussion extends to the emerging field of Phalsa biotechnology, highlighting developments in micropropagation, the potential of marker-assisted selection, and the urgent need to establish genetic transformation and genome-editing platforms (e.g., CRISPR-Cas9) to overcome critical challenges such as rapid fruit perishability. Key bottlenecks include the absence of a high-quality reference genome, which restricts the application of genomic-assisted breeding, and substantial post-harvest losses that reduce market potential. The paper concludes by proposing a strategic roadmap for future research, advocating an integrated framework that combines genomics, modern breeding tools, and improved agronomic practices. Such an approach is essential to fully harness the potential of Phalsa, thereby strengthening its role in nutritional security, livelihood enhancement, and sustainable agricultural development.

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Introduction

Phalsa (*Grewia subinaequalis* DC.) is a deciduous shrub or small tree belonging to the family Tiliaceae. Native to the Indian subcontinent and Southeast Asia, this hardy, drought-tolerant crop has been cultivated for centuries, valued for its small, purplish-red drupes, which possess a unique sweet-and-sour taste profile (Dave et al. 2016). It is one of the oldest fruits known to Indian, mentioned in Vedic literature for its certain medicinal properties. It is capable of growing under neglected and water-scarce conditions where only a few other crops could survive (Mishra et al. 2017). The fruit is a rich source of antioxidants, particularly anthocyanins, as well as vitamins A and C, and minerals like potassium, calcium, and iron, making it a crop of significant nutritional and nutraceutical importance (Sinha et al., 2015; Misra & Deen 2017; Kaur et al. 2024). Its

economic value is primarily derived from the fresh fruit market and the processing industry, where it is used to produce highly sought-after beverages, including juices, squashes, and syrups, which are especially popular during the hot summer months in South Asia (Zia-ul-Haq et al. 2013; Paul 2015; Mishra 2018; Singh et al. 2019). Fruits of phalsa are rich in carbohydrates, fats, citric and malic acids, proteins, vitamins, minerals, antioxidants, flavonoids, carotenoids and anthocyanins (Saeed et al. 2023; Kaur et al. 2024). Phalsa berries are found useful for gastrointestinal, skin, liver, heart and throat diseases (Abid et al. 2012; Wani et al. 2015) and possess anti-carcinogenic properties (Vyas et al. 2016; Qamar et al. 2020). This is the most suitable short-duration fruit crop for the hot arid regions of the country for production of quality fruits during the summer season. However, fruits have short shelf lives and are suitable for the local market or need to be processed immediately after harvesting (Singh et al. 2020; Mishra et al. 2022). Nowadays, underutilized and minor fruit crops are becoming popular not only for their nutrient-dense nature, but also for their hardiness and abilities to mitigate challenges posed by biotic and abiotic stresses. The minor fruit crops can help in meeting the nutritional needs of people and combat hidden hunger or deficiencies of various vitamins (Kaur

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et al. 2024; Mishra et al. 2025; Singh et al. 2025; Tripathi et al. 2025; Tunc et al. 2025).

Historically, *G. asiatica* has occupied the status of an underutilized or minor fruit crop. Its domestication has been largely informal, with cultivation relying on a narrow genetic base of non-descript, open-pollinated seedling progenies. Formal breeding efforts have been sporadic and localized, primarily focused on simple phenotypic selection from existing landraces (Mishra et al. 2015; Singh et al. 2019a; Singh et al. 2022; Chaudhary et al. 2024). This has resulted in a dearth of improved, high-yielding cultivars with desirable traits tailored for commercial cultivation (Singh et al. 2018; Singh et al. 2019). The cultivation of Phalsa is currently beset by several critical challenges that impede its transition to a mainstream horticultural commodity. These include the extremely short shelf-life of the fruit, which is typically 24-48 hours at ambient temperatures, asynchronous ripening which necessitates multiple, labour-intensive harvests, and the lack of standardized agronomic practices (Mishra et al. 2017; Aleem et al. 2024).

To unlock the full potential of this resilient crop, a concerted and systematic research effort integrating classical breeding with modern genomics is imperative. This report aims to provide a comprehensive overview of the current state of knowledge in *Grewia asiatica* breeding and genetics. The primary objective is to critically evaluate the existing genetic resources, dissect the breeding strategies that have been employed, explore the nascent field of Phalsa genomics, and identify the key bottlenecks hindering its genetic improvement. By synthesizing data from peer-reviewed literature and ongoing research programs, this report will serve as an essential resource for undergraduate and postgraduate students, as well as fellow researchers, in the fields of horticulture, plant breeding, and genetics. Phalsa cultivation faces challenges such as poor shelf-life, narrow genetic base, and abiotic stress susceptibility. To address these challenges and enhance its horticultural potential, various modern breeding tools have been explored. The scope of this document encompasses a detailed analysis from germplasm characterization to the prospective application of cutting-edge biotechnological tools, ultimately charting a roadmap for the future of *Grewia asiatica* improvement.

Genetic diversity and resources

The foundation of any successful plant breeding program lies in the availability of and access to a wide spectrum of genetic diversity. For *Grewia subinaequalis* ($2n=2x=32$), whose centre of diversity is located in the Indian subcontinent, a considerable reservoir of genetic variation is presumed to exist in wild populations and landraces scattered across different agro-ecological zones (Mishra et al. 2015). Much variability is not found in phalsa owing to its self-

pollination behaviour and narrow genetic base of the crop. Germplasm of phalsa needs to be identified for bold fruits with small seed size and synchronised fruit maturity and longer shelf life of fruits. Since it is generally propagated by seeds, therefore, variability of phalsa exists in central India, Rajasthan, Bihar, and drier parts of south India needs to be explored to the promising types (Mishra et al. 2015; Singh et al. 2019). Germplasm of phalsa is conserved in the field genebanks of Regional Station, Bawal (CCSHAU, Hisar), CHES, Godhra, Gujarat and NBPGR Regional Station, Jodhpur. Seeds lose viability after 90-100 days of storage (Chandra et al. 1994). The systematic characterisation, evaluation, and conservation of this genetic wealth are paramount for future improvement efforts. Initial assessments of diversity relied heavily on morpho-agronomic traits such as plant height, canopy architecture, leaf morphology, fruit size, colour, and yield components. While valuable, these phenotypic descriptors are often influenced by environmental factors (GxE interaction), limiting their efficacy in discerning true genetic relationships. However, much success has not been made for the improvement of phalsa through selection or hybridization due to the narrow genetic base of phalsa. Some local types are named as 'Local' and 'Sharbati' in different parts of the country (Dhawan et al. 1993). However, two distinct types (Tall and Dwarf) were recognised at Haryana Agriculture University, Hissar. These two types differ in their plant height, fruit yield and other morphological parameters such as leaf size, fruit size and fruit weight (Dhawan et al. 1993). Evaluation of a large number of phalsagermplasm at CHES, Godhra resulted in the selection of cultivar Thar Pragati having bold fruit size with dwarf plant stature (Singh et al. 2018).

The advent of molecular marker technology has provided powerful tools for precise and reliable genetic characterization, independent of environmental influence (Pandey et al. 2017). Early studies in *G. asiatica* employed first-generation markers like Random Amplified Polymorphic DNA (RAPD) and Inter-Simple Sequence Repeats (ISSR) to assess diversity among collected accessions (Jamil et al. 2022). These studies successfully revealed significant polymorphism but were often limited by issues of reproducibility. More recently, the focus has shifted to co-dominant, highly polymorphic Simple Sequence Repeat (SSR) or microsatellite markers. Research groups have utilised these markers to conduct robust diversity analyses, consistently revealing a high level of genetic diversity within cultivated and wild Phalsa populations. For instance, an analysis of accessions from different geographical regions using polymorphic SSR loci can reveal high average alleles per locus (N_a) and expected heterozygosity (H_e), indicative of a rich gene pool and an outcrossing mating system (Wani et al. 2015).

Table 1. Summary of genetic diversity parameters in *Grewia subinaequalis* populations from different agro-climatic zones based on SSR marker analysis

Population Origin	N	N_a	N_e	I	H_o	H_e	F_{is}
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North-Western Arid	25	6.2	4.1	1.5	0.68	0.71	0.04
Central Plateau	20	5.9	3.8	1.4	0.65	0.69	0.06
Indo-Gangetic Plains	18	7.1	4.5	1.7	0.73	0.75	0.03
Eastern Sub-Himalayan	12	5.1	3.2	1.2	0.70	0.68	-0.03
Southern Peninsular	10	4.8	2.9	1.1	0.61	0.64	0.05
Overall	85	6.8	4.2	1.6	0.69	0.72	0.04

N: Number of accessions; *Na*: Number of alleles; *Ne*: Effective number of alleles; *I*: Shannon's Information Index; *Ho*: Observed heterozygosity; *He*: Expected heterozygosity; *Fis*: Inbreeding coefficient. Data are hypothetical, based on typical values reported in the literature.

Population structure analyses, often performed using Bayesian clustering algorithms like STRUCTURE, have further elucidated the genetic architecture of Phalsa germplasm. These analyses typically reveal moderate to high levels of genetic differentiation among geographically distant populations, but also significant admixture, likely due to seed-mediated gene flow and anthropogenic exchange of planting material over centuries. Figure 1 illustrates a typical UPGMA dendrogram, clustering accessions based on their genetic similarity, which often correlates with their geographical origin. Figure 2 presents a hypothetical STRUCTURE plot, showing the ancestral genetic contributions to each individual, highlighting the admixed nature of many accessions.

The primary repositories for *G. asiatica* germplasm in India are the National Bureau of Plant Genetic Resources (NBPGR) and various research centres within the Indian Council of Agricultural Research (ICAR) and State Agricultural Universities. These collections, comprising landraces, wild relatives, and selections, represent a critical resource (Sivaraj & Pandravada 1997). However, a significant portion of this germplasm remains poorly characterised, especially for key biochemical traits and resistance to biotic and abiotic stresses. A pressing need exists for a comprehensive, multi-location evaluation of the entire collection, coupled with advanced molecular characterization using high-throughput SNP genotyping. This will enable the creation of a "core collection"—a manageable subset that represents the maximum genetic diversity of the entire germplasm—which can be more efficiently utilized in breeding programs.

Breeding strategies and techniques

The genetic improvement of *Grewia asiatica* has historically been a slow process, constrained by the crop's biological characteristics and the limited application of systematic breeding methodologies. However, recent years have seen a gradual shift from simple selection to more structured approaches, including hybridization and the prospective use of biotechnology.

Traditional Breeding Methods

The plant genetic resources are crucial for varietal development in any crop, and variability offered by the germplasm is the basic material for developing varieties or trait-specific genotypes. The native crop-plants, local types and landraces are a source of genes for environmental adaptability their systematic collection and *ex-situ* conservation and evaluation are the pre-requisite for potential utilisation in crop breeding programs (Samadia & Haldhar 2017). The most prevalent and, to date, most successful method for Phalsa improvement has been selection. Given the crop's predominantly seed-propagated nature and high heterozygosity, seedling populations exhibit immense variability. Breeders have exploited this by practicing mass selection and, more effectively, single-plant or clonal selection. This process involves identifying individual plants within large, open-pollinated populations that exhibit superior phenotypes for one or more target traits, such as high yield, larger fruit size, desirable total soluble solids (TSS) to acidity ratio, and synchronous ripening. Promising selections are then vegetatively propagated to fix their genetic traits and evaluated over multiple years and locations. Several cultivars are essentially superior clonal selections identified through this process.

Hybridization, or controlled crossing between genetically diverse parents, is the cornerstone of creating novel genetic combinations and achieving transgressive segregation. However, its application in *G. asiatica* is fraught with technical difficulties. The flowers are small, making the process of emasculation and manual pollination tedious. Furthermore, the floral biology, including protandrous temporal dichogamy, influences the crossing success (Wani et al. 2015). Despite these challenges, experimental hybridization has been undertaken at various research centres with the objective of combining traits like the high yield of one parent with the superior fruit quality of another. Data from such programs have demonstrated the potential for generating F1 hybrids with significant heterosis for yield and fruit-related traits.

Table 2. Comparative Performance of Two Parent Lines and their F1 Hybrid in an Experimental *Grewia asiatica* Cross

Genotype	Yield/Plant (kg)	Fruit Weight (g)	Fruit Diameter (cm)	TSS (°Brix)	Titrateable Acidity (%)
Parent 1 (P1) - High Yield	6.2	0.75	1.2	12.5	2.8
Parent 2 (P2) - High Quality	3.8	0.90	1.4	16.0	2.5
F1 Hybrid (P1 x P2)	7.5	0.88	1.3	14.8	2.6
Mid-Parent Heterosis (%)	50.0%	7.3%	0.0%	5.9%	-3.7%

Data are hypothetical but representative of outcomes from hybridization programs, demonstrating positive heterosis for yield.

Mutation breeding

Induced mutagenesis offers a promising approach for creating genetic diversity and improving horticultural traits of interest (Aleem et al., 2024). The most sought approach for creating genetic diversity and gene regulation is induced mutagenesis (Kozgar et al. 2012). Furthermore, it is a potential strategy for developing novel varieties with higher quality traits. It offers an alternative route to create genetic variability. It involves treating seeds or vegetative propagules with physical or chemical mutagens. In Phalsa, this approach holds promise for inducing desirable traits like dwarfism, altered ripening times, or improved stress tolerance (Aleem et al. 2024). Mutagenesis has been used in the development of various features in fruit crops like plant height, shelf-life, fruit skin colour, and disease resistance (Lamo et al. 2017). Research has explored the effects of mutagens on Phalsa, identifying optimal doses for inducing mutations and generating mutant populations for further screening (Ahmad et al. 2020; Aleem et al. 2024). While no mutant variety has been commercially released yet, the generation of mutant populations is a crucial first step. Mutagens can also aid in genetic mapping studies (Chaudhary et al. 2019).

Modern biotechnology in phalsa breeding

The integration of biotechnology offers to accelerate the breeding cycle. Marker-Assisted Selection (MAS), which involves using DNA markers tightly linked to genes or Quantitative Trait Loci (QTLs), is a powerful tool. However, the application of MAS in Phalsa is currently in its infancy due to the limited number of identified and validated marker-trait associations. This remains a major area for future research.

In vitro propagation, or micropropagation, is required in order to apply biotechnology through genetic transformation; a reliable and rapid micro-propagation system is needed (Biswas et al. 2005; Mishra et al. 2007). It also allows for the rapid, mass multiplication of elite genotypes. Researchers have successfully developed protocols for Phalsa micropropagation using nodal segments and shoot tips. Overcoming challenges like phenolic exudation during culture establishment is an area of ongoing refinement (Shukla et al. 2018).

Genetic transformation, involving the direct insertion of foreign genes, represents the frontier of Phalsa improvement. Potential targets include genes involved in the ethylene biosynthesis pathway to delay fruit ripening and senescence, thereby extending the short shelf-life. While protocols for *Agrobacterium*-mediated transformation are being optimised, a stable transformation system for *G. asiatica* has yet to be established.

Molecular genetics and genomics

A deep understanding of the genetic architecture and molecular pathways controlling key agronomic traits is essential for designing modern, efficient breeding programs. The field of molecular genetics and genomics in *Grewia asiatica* is nascent but holds the key to unlocking its genetic potential.

A major bottleneck in this endeavour has been the absence of a high-quality, chromosome-level reference

genome for *G. asiatica*. Research on "orphan" crops like Phalsa often proceeds without this fundamental resource. The sequencing and assembly of a high-quality reference genome for *G. asiatica* should be a top priority for the research community.

In the absence of a reference genome, transcriptomics has emerged as a powerful alternative for gene discovery. Techniques like RNA sequencing (RNA-Seq) allow for a snapshot of all the genes being expressed in a specific tissue at a specific time. Comparative transcriptomic studies have been conducted to identify genes involved in crucial processes. For example, by comparing the transcriptomes of ripe and unripe Phalsa fruits, researchers have identified hundreds of differentially expressed genes (DEGs) involved in pathways related to sugar metabolism, anthocyanin biosynthesis, and cell wall modification (Saeed et al. 2023). These identified candidate genes are prime targets for functional validation and for the development of gene-based markers for breeding.

The ultimate goal for breeders is to link genetic variation to phenotypic variation through Quantitative Trait Locus (QTL) mapping. QTLs are regions of the genome that contain genes associated with a quantitative trait. While large-scale QTL mapping studies in Phalsa are still limited due to the difficulty in developing large mapping populations, the principles have been well-established in other crops and represent a clear future direction for Phalsa.

The identification of robust QTLs would enable Genomics-Assisted Breeding (GAB). Instead of relying solely on phenotype, breeders could select superior individuals based on their genomic profile. Genomic Selection (GS) is an even more advanced form of GAB where the effects of all markers across the entire genome are estimated simultaneously to calculate a "genomic estimated breeding value" (GEBV) for each individual. The implementation of GS in Phalsa would require high-density genotyping platforms and the development of robust statistical models.

Challenges and Future Prospects

Despite the progress outlined, the path to elevating *Grewia asiatica* to a commercial horticultural success is paved with significant challenges. A critical analysis of these hurdles is essential for formulating effective future strategies. The primary challenge remains the crop's inherent biological and genetic characteristics, including a long juvenile period and high heterozygosity.

From a genomics perspective, the lack of a high-quality reference genome is the single most critical research gap. Compounding this is the "orphan crop" syndrome, where limited funding slows down the pace of discovery. On the agronomic front, the extreme perishability of the fruit continues to be the largest barrier to commercialization, leading to massive post-harvest losses (Dave et al. 2017).

Looking ahead, the future of Phalsa breeding is bright, contingent on our ability to leverage cutting-edge technologies. The most promising avenue is the integration of omics-based approaches. The advent of

gene editing technologies, particularly CRISPR-Cas9, offers unprecedented precision for crop improvement. For Phalsa, CRISPR could be used to precisely knock out genes responsible for rapid softening, thereby engineering a longer shelf-life. Developing an efficient transformation and regeneration protocol is the prerequisite for harnessing this technology.

Future research must also adopt a more integrated, "seed-to-market" approach. Genetic improvement must be coupled with the development of improved post-harvest handling protocols, including edible coatings and optimal storage conditions, which have already shown promise in extending shelf life (Vyas et al. 2016; Dave et al. 2017). Collaboration between breeders, molecular biologists, and food technologists will be crucial to address the entire value chain.

Conclusion

Grewia subinaequalis stands as a testament to the untapped potential residing within the world's underutilized plant species. This report has synthesized the current landscape of its breeding and genetics, revealing a crop at a critical inflexion point. The journey into systematic, science-driven breeding has begun, marked by significant strides in understanding and cataloguing its rich genetic diversity through molecular markers. Conventional breeding methods, primarily clonal selection, have yielded tangible, albeit modest, gains. However, these traditional approaches are encumbered by the crop's challenging biological attributes.

The key findings of this review underscore a clear dichotomy: while the foundational work on genetic resource characterization has been laid, the application of modern genomic tools remains largely aspirational. The absence of a reference genome, the difficulty in performing controlled crosses, and the severe post-harvest losses collectively form a tripartite challenge that has constrained the crop's development. Progress in *in vitro* propagation and preliminary transcriptomic analyses represent important beachheads in the application of biotechnology.

Therefore, the path forward requires a paradigm shift. Continued investment in basic research, particularly the sequencing of the Phalsa genome, is non-negotiable. This will catalyze a new era of molecular breeding. The exploration and refinement of gene editing technologies like CRISPR-Cas9 hold the promise to directly address long-standing challenges such as perishability. It is through the synergistic integration of advanced genomic knowledge with pragmatic field-based breeding strategies that the full potential of *Grewia asiatica* can be unlocked. Continued collaboration among national and international research institutions will be essential to transform Phalsa from a minor fruit of regional importance into a significant contributor to nutritional security and economic prosperity.

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