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INTEGRATING MOLECULAR AND BIOCHEMICAL APPROACHES FOR JACKFRUIT (*ARTOCARPUS HETEROPHYLLUS* LAM.) GERMPLASM CHARACTERIZATION: A REVIEW

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ABSTRACT:
Artocarpus heterophyllus Lam. (jackfruit) is an important tropical fruit species due to its nutritional value, economic value, and ecological importance. Due to its widespread presence throughout South and Southeast Asia, it is, however, less utilized genetically than many other major tropical fruit species. While several independent studies have examined both the molecular diversity and biochemical characteristics of the germplasm of jackfruit, there has not yet been an inclusive integration of these two methodologies. The purpose of this review is to evaluate the progression of molecular characterization starting with random amplified polymorphic DNA (RAPD) and inter-simple sequence repeat (ISSR) markers followed by simple sequence repeats (SSRs) and then genome-wide single nucleotide polymorphism (SNP) discoveries as well as recent chromosome-scale genome assembly. In addition to evaluating the advancements in molecular characterization, this review also evaluates the progress in biochemical characterization which includes nutritional composition, phytochemical/antioxidant diversity, seed protein/isozyme variation, starch properties/lipid composition and volatile aroma profiles. Rather than treat each area of research independently, this review analyzed how molecular data can be used to complement biochemical data, identified discrepancies among studies and highlighted the methodological limitations that have prohibited direct comparison of the germplasm collections. The available evidence demonstrated significant genetic and biochemical variability within jackfruit that is significantly associated with geographic location, but demonstrated that multi-disciplinary analysis of germplasm panels are still relatively rare. Recent developments in genomic resources offer an unprecedented opportunity to link these disciplines at a high-resolution using genetics with comprehensive datasets of phenotype and biochemistry. Future work would include population scale SNP genotyping, marker-trait associations, untargeted metabolomics and establishment of a well-characterized core collection of germplasm representing the genetic diversity of the species, moving beyond the current focus on Indian accessions.

KEYWORDS: *Artocarpus heterophyllus;* germplasm diversity; molecular markers; phytochemicals; South Asia

1. INTRODUCTION

Jackfruit (*Artocarpus heterophyllus* Lam.) is the world's largest tree-borne fruit and is native to the Western Ghats of India. Its versatility, high productivity, and adaptability have led to its widespread cultivation in South and Southeast Asia as well as in tropical Africa, Oceania and part of the Americas (1, 2). Due to its high carbohydrate content, dietary fibre, vitamins, minerals and variety of bioactive compounds, jackfruit has been receiving more attention in recent years and considered as an underutilized fruit crop with great potential to be utilized in food and nutrition security (3, 4). Beyond fresh fruit consumption, immature jackfruit has been recognized as a potential plant-based meat substitute, while its seeds and processing by-products are gaining attention for their nutritional value and industrial applications (4, 5).

South Asia is the major region of diversity for jackfruit, as India, Bangladesh and Sri Lanka harbour high genetic diversity of the species, which is attributed to its long history of natural selection, cross-pollination and farmers' selection. Due to the predominantly outcrossing nature of jackfruit, highly heterogeneous populations with great variation with respect to tree architecture, fruit morphology, pulp colour, texture, flavour, yield potential and nutritional composition have been observed (6, 3). Despite all this diversity, jackfruit has received comparatively little scientific attention in terms of systematic breeding programmes, genomic resource development and germplasm characterization, as compared to other tropical fruit crops like mango, citrus and banana. Several invaluable landraces are poorly characterized and underutilized, thus the need for germplasm evaluation and conservation in a systematic manner is highlighted (7).

Crop improvement and genetic resource management rests on the basis of a comprehensive characterization of germplasm. Morphological descriptors can give important information on phenotypic variation, but can also be affected by environmental factors and developmental stage. Molecular marker technologies, on the other hand, allow the direct assessment of genetic diversity without the influence of environmental factors. Biochemical profiling data, in turn, can be used to complement these approaches and provide information on differences in nutritional composition and other phytochemicals and metabolites related to fruit quality and functional properties (8, 9). The integration of the three types of data, namely the morphological data, the molecular and biochemical data, therefore, allows not only for a more comprehensive understanding of germplasm diversity but also for selecting elite accessions for breeding, conservation and commercial use.

In recent years, jackfruit research has shifted from traditional marker-based studies towards high-resolution genomic studies with the advancement of molecular genetics. With the support of draft and whole-chromosomal genome assemblies and next generation sequencing (NGS) technologies, single nucleotide polymorphisms (SNPs) were identified throughout the genome, comparative genomics and candidate gene identification were performed for economically important traits (10, 11, 12). These genomic resources will contribute to the speeding up of molecular breeding and open new avenues for the conservation and sustainable use of jackfruit genetic resources.

This review aims to critically evaluate recent advances in molecular and biochemical characterization of jackfruit germplasm and highlight their applications in conservation and breeding. It discusses the use of RAPD, ISSR and SSR-based marker systems to assess the nutritional and phytochemical diversity and their integration in germplasm conservation, molecular breeding, and future crop improvement strategies, while discussing biochemical approaches to assess nutritional and phytochemical diversity. (Fig.1)

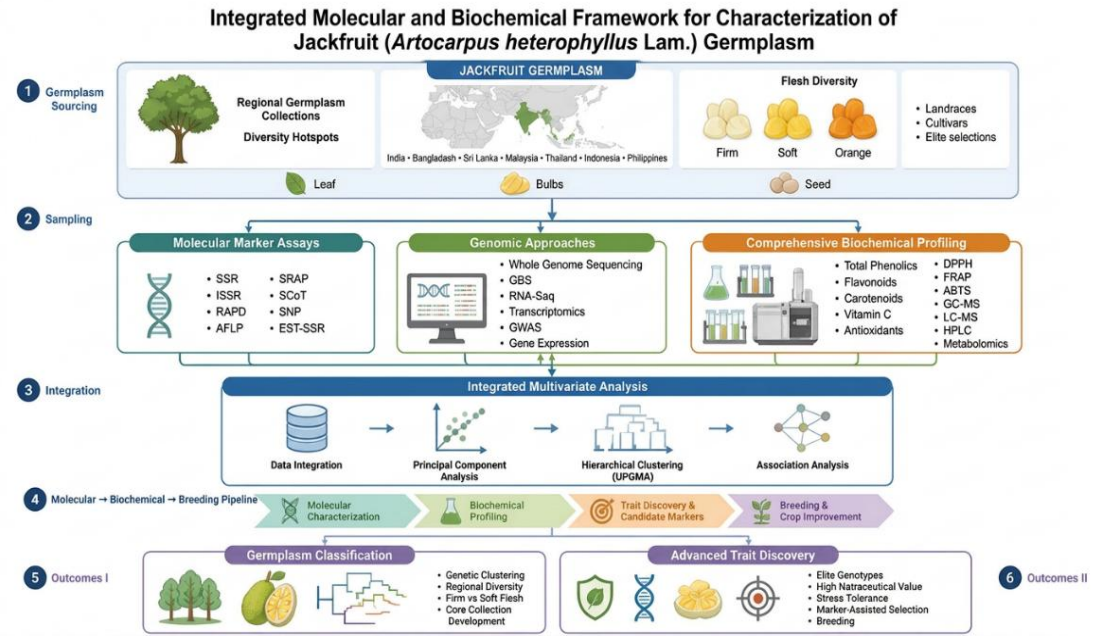

Fig. 1. Conceptual framework for integrated molecular and biochemical characterization of jackfruit germplasm. The workflow encompasses germplasm collection, DNA extraction, molecular marker analysis (SSR, RAPD, ISSR, SNP/NGS), biochemical profiling (nutritional, phytochemical, enzyme, fatty acid, volatile), integrated data analysis, and applications in conservation and breeding

2. Taxonomic and Botanical Overview of Jackfruit

The jackfruit (*Artocarpus heterophyllus* Lam.) belongs to the family Moraceae, which comprises approximately 40 genera and over 1,000 species distributed mainly in tropical and subtropical regions. There are over 70 species in the genus Artocarpus R.Br. that are found across tropical Asia, including A. heterophyllus Lam. being the most economically important species (3). A. integer, A. altilis (breadfruit) and A. lakoocha (monkey jackfruit) are close relatives, sharing genetic and biochemical characteristics that are relevant and beneficial to phylogenetic and comparative genomics studies (14, 15).

The monoecious, evergreen jackfruit tree reaches a height of 8 to 25 m and is a latex producing tree. The largest tree fruit in the world, the syncarp (complex fruit) can weigh anywhere from 1 to 50 kg and is created when hundreds of individual blossoms fuse together (16). A. heterophyllus primarily comprises two main types: the “varikka” type (firm/crisp flesh) and the “koozha” or “koozha chakka” type (soft/melting flesh) with fibrous, juicy perianths (17, 18). The morphological and agronomic attributes (fruit weight, rind texture and flesh colour) of ten representative accessions from these regions are summarised in Table 1. These pronounced morphological differences are useful phenotypic correlates for molecular characterization, as they are associated with variation in underlying biochemical composition and are, in part, under genetic control.

Table 1. Morphological and agronomic characteristics of selected jackfruit accessions from South Asia

Germplasm / Ecotype	Region	Distinguishing characteristics	Major utilization	Reference
Varikka (firm-fleshed type)	Kerala, India	Firm, crisp bulbs; thick carpels; high edible portion; preferred for table use	Fresh consumption	(3)
Koozha (soft-fleshed type)	Kerala, India	Soft, fibrous, juicy bulbs with strong aroma	Processing and household consumption	(3)
Waraka	Sri Lanka	Firm-textured bulbs with low latex and good eating quality	Fresh market	(19)
Vela	Sri Lanka	Soft, juicy bulbs with characteristic flavour	Fresh and processed products	(19)
Khaja	Bangladesh	Firm, crisp pulp with high consumer preference	Dessert fruit	(6)
Baromashi	Bangladesh	Extended or off-season bearing habit	Year-round production	(6)

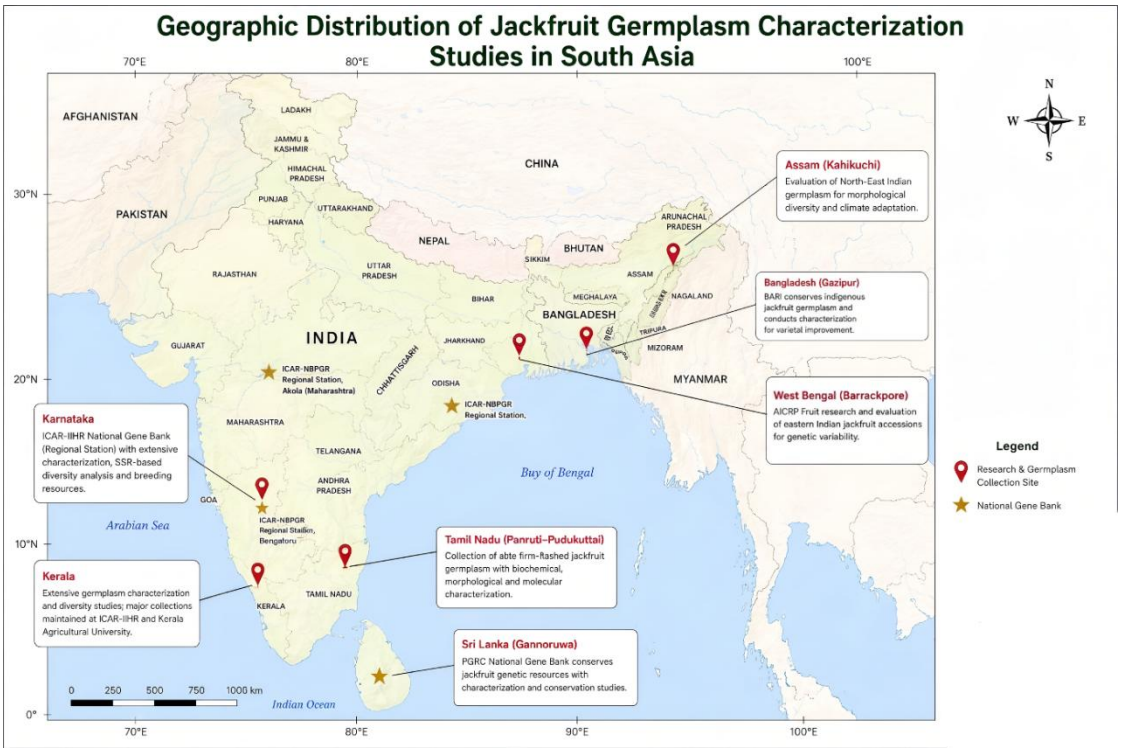

Fig. 2. Geographic distribution map of jackfruit germplasm characterization studies in South Asia. Points represent major collection sites and research stations in India (Kerala, Tamil Nadu, Karnataka, West Bengal, Assam), Sri Lanka, and Bangladesh, colour-coded by country. Major gene bank locations are indicated by distinct symbols.

The Western Ghats of India are the primary center of diversity of jackfruits, and the highest proportion of wild and semi-wild varieties are found here (20). However, there is a significant diversity in Bangladesh and north-eastern India while Sri Lanka is a secondary centre of diversity (19, 21). The geographical distribution of the germplasm in South Asia with emphasis on concentration of important germplasm collection sites and described accessions is depicted in Fig. 2 (13).

3. Molecular Characterization of the Germplasm of Jackfruit

With molecular characterization, the genetic variation can be assessed directly at the DNA level, which is not affected by environmental or developmental conditions, and thus has become an indispensable tool for germplasm characterization (22, 23). Molecular markers are useful tools for estimating genetic diversity, detecting duplicate accessions and deciphering population structure. They are also valuable for breeding and conservation programmes in jackfruit (*Artocarpus heterophyllus* Lam.), a mostly cross-pollinated species with high heterozygosity and wide phenotypic diversity (24, 25, 26). DNA-based markers allow discrimination between closely related genotypes with high fidelity and repeatability, whereas conventional morphological descriptors are easily influenced by environmental variations (27).

In the last 3 decades, molecular characterization of jackfruit has shifted from the predominant markers used earlier like Random Amplified Polymorphic DNA (RAPD) and Inter-Simple Sequence Repeat (ISSR) to co-dominant Simple

Sequence Repeat (SSR) markers and then to genome-wide Single Nucleotide Polymorphism (SNP) markers produced by the next generation sequencing (NGS) technologies (28, 29, 22, 30, 26). These advances have significantly improved the resolution, reliability and throughput of genetic characterization in jackfruit germplasm.

3.1 Simple Sequence Repeat (SSR) Markers

The simple sequence repeat (SSR) or microsatellite markers are the most informative conventional marker system that have been adopted for the characterization of germplasm in many fruit crops due to their codominant inheritance, high polymorphism information content (PIC), repeatability, and multiplexing amenability (23, 22). Because of their co-dominant, multi-allelic, locus-specific, and highly reproducible nature, simple sequence repeat (SSR) markers are now the basic molecular marker used for the genetic study of jackfruit (*Artocarpus heterophyllus* Lam.) as these markers provide better resolution than the dominant RAPD markers for cultivar fingerprinting, diversity assessment and marker-assisted selection (MAS) (25, 31). Initial uses of SSRs were limited to a brief list of markers (including cross-species transferable primers from related Artocarpus and Moraceae taxa) and showed that even a basic SSR panel could yield a unique banding pattern for varietal authentication (32, 33). Of the 50 SSR primers screened, 11 were found to be polymorphic. Among these, MAA145 detected 100% polymorphism with a PIC of 0.40 (overall SSR PIC range 0.22-0.98). These markers yielded robust DNA fingerprints for released varieties such as Sindhur and other elite selections in Kerala (33).

In southern Karnataka, a study (25) screened 35 SSR markers (22 of which were found to be amplifying) across 20 genotypes and identified six most informative markers (SSR9, SSR10, SSR30, SSR34, SSR45 and SSR48) which separated unweighted pair group method with arithmetic mean (UPGMA) clusters corresponding to pulp colour classes, demonstrating that these markers can support trait-based classification of germplasm and help breeders select parental lines with contrasting pulp colour for targeted crosses. The introduction of next generation sequencing (NGS) greatly increased the number of jackfruit marker resources available, with another study (31) identifying 16,853 perfect genic SSRs and 142 alleles (3.74 alleles per SSR) from transcriptome data, which were confirmed as polymorphic by screening 224 accessions, with a mean PIC value of 0.47, 4 genetic groups, and ≈90% variation within groups, suggesting high levels of outcrossing and gene flow in Eastern and North Eastern India. High allelic richness within the populations and strong within population diversity has been observed in complementary studies using six SSR in Kenya and Ugandan populations (34) and 20 microsatellites in elite Karnataka trees (35) while comprehensive SSR assays in elite Kerala accessions have begun to identify associations between markers and various traits, including β carotene and total sugar, supporting the continued importance of SSRs in jackfruit germplasm management and targeted breeding for desirable traits (36). Representative SSR marker studies in jackfruit are summarised in Table 2.

Table 2. Characteristics of selected SSR markers applied to jackfruit germplasm characterization

Study	SSR Marker(s)	Major Findings	Application
(33)	11 polymorphic SSR loci (MAA145 most informative)	PIC ranged from 0.22–0.98; MAA145 showed complete polymorphism and generated variety-specific DNA fingerprints for elite Kerala cultivars.	Variety identification and DNA fingerprinting
(25)	SSR9, SSR10, SSR30, SSR34, SSR45, SSR48	Six polymorphic SSR markers differentiated 20 genotypes according to pulp colour and produced three major genetic clusters.	Germplasm characterization and diversity analysis
(32)	Seven transferable SSR markers	Cross-species amplification yielded 6–17 alleles per locus with PIC values of 0.73–0.89, demonstrating high transferability within Artocarpus.	Marker transferability and comparative genomics
(31)	38 transcriptome-derived genic SSRs	Developed 16,853 SSR loci; 38 polymorphic markers generated 142 alleles (3.74 alleles locus^{-1}) with PIC 0.25–0.69, revealing four genetic groups and 90% within-population variation.	Population genetics, conservation and molecular characterization
(36)	38 polymorphic SSR markers	Identified three genetic sub-populations, 142 putative alleles, and significant marker–trait associations for β-carotene and total sugar.	Marker-assisted breeding and trait mapping
(35)	20 microsatellite markers	Generated 192 alleles (9.6 alleles locus^{-1}) with PIC values of 0.428–0.930, revealing high allelic diversity among elite Karnataka accessions.	Germplasm characterization and diversity assessment

3.2 RAPD Markers

Random amplified polymorphic DNA (RAPD) markers were one of the first molecular markers used for genetic characterization of jackfruit (*Artocarpus heterophyllus* Lam.) and remain useful in laboratories where low operational costs, low-quality DNA inputs, and minimal labor requirements are prioritized. RAPD markers are dominant, but can be influenced by PCR conditions, and have made significant contributions to genetic diversity studies, cultivar identity, clonal fidelity and fruit-type discrimination (37, 28). One study (38) examined 12 high-yielding accessions, producing 171 reproducible fragments from 23 RAPD primers, and 67.3% of the fragments were polymorphic. The RAPD markers were useful for the differentiation of Kerala and Karnataka accessions using cluster analysis, which showed geographical origin and pulp texture.

Likewise, one study (40) screened 20 jackfruit genotypes of four pulp-colour classes with 20 RAPD primers, which showed moderate genetic variability with high polymorphism information content (PIC) of up to 0.31 and found some RAPD primers to be informative for differentiation in pulp-colour. Another study (39) also showed that RAPD markers could be used effectively for discriminating leaf accessions of different phytochemical groups on the basis of banding patterns. In addition, RAPD has been used in applied breeding; one study (41) used a fruit-type-specific RAPD fragment to differentiate hard- and soft-fleshed jackfruit, while another study (42) provided complete genetic uniformity among micropropagated plants by using clonal fidelity analysis based on RAPD. Although co-dominant markers like SSRs and high-density SNP markers have replaced RAPD, RAPD is still a rapid and inexpensive screening tool for preliminary assessment of genetic diversity and germplasm management, especially in conjunction with other more powerful markers. Representative RAPD marker studies are summarised in Table 3.

Table 3. Representative RAPD marker studies and their applications in jackfruit molecular characterization

RAPD Analysis	Plant Material	Major Findings	Application	Reference
23 primers; 171 bands	12 high-yielding accessions	67.3% polymorphism; clustered accessions by geographical origin and pulp texture	Germplasm characterization	(38)
2 primers (OPA-8, OPA-9)	5 leaf accessions	57 bands with unique polymorphic fragments differentiating phytochemically distinct accessions	Genetic diversity assessment	(39)
20 primers	20 genotypes	Moderate genetic diversity; PIC up to 0.31; differentiation based on pulp colour	Diversity analysis and cultivar characterization	(40)
100 primers	70 Sri Lankan accessions	Identified fruit-type-specific RAPD marker (OPB-01, ~1 kb) distinguishing hard- and soft-fleshed types	Early fruit-type identification	(41)
15 primers	11 micropropagated plants	All loci monomorphic with similarity coefficient of 1.00, confirming clonal fidelity	Genetic stability assessment	(42)

3.3 Inter-Simple Sequence Repeat (ISSR) Markers

Inter-simple sequence repeats (ISSRs) are an important alternative to RAPD markers for molecular characterization of jackfruit (*Artocarpus heterophyllus* Lam.) as they offer increased reproducibility, increased polymorphism and do not require any prior sequence information. ISSR is also useful for genetic diversity studies, differentiation of cultivars and population structure analysis in resource-constrained breeding programmes, due to their capacity to amplify multiple genomic loci using microsatellite-anchored primers. One study (43) genotyped the jackfruit germplasm from Kerala with 50 ISSR primers, resulting in 86 amplification products with 55% of the primers being informative. The five major groups with 77% similarity clearly separated accessions based on pulp texture.

Recently, a later study (44) identified 30 accessions from the North Kerala region in the off-season using a combination of ISSR and SSR markers. The ISSR primers had an average polymorphism information content (PIC) of 0.146 and an average expected heterozygosity of 0.205 with 65.3% polymorphism, the district-wise population structure was resolved and the distinct accession KNR-1 with a low-glycaemic-index fruit was identified by integrated marker analysis. As for the applications of ISSR outside of South Asia, a study (45) found 52 amplified fragments and 51.9% polymorphism in six landraces of Egypt, and the ISSR-based clustering was found to be quite similar to the morpho-chemical clustering. Methodological developments have also enhanced the applicability of ISSR, with another study (46) optimizing the DNA extraction and amplification protocol for polyphenol rich jackfruit tissues. All the above-mentioned studies highlight that the ISSR markers have the ability to provide useful and inexpensive platform for germplasm characterization, cultivar discrimination, population genetics and population-based diversity analysis in jackfruit improvement programmes in addition to the SSR and SNP markers. Selected ISSR primers and their polymorphism levels are summarised in Table 4.

Table 4. Selected ISSR primers and their polymorphism in jackfruit germplasm studies

Plant Material	ISSR Analysis	Major Findings	Application	Reference
Kerala jackfruit germplasm	50 primers screened; 10 informative ISSR primers selected	Generated 86 bands with 55% polymorphism; resolved five genetic clusters (77% similarity) and differentiated firm- and soft-fleshed accessions	Germplasm characterization and cultivar discrimination	(43)
Six Egyptian landraces	10 ISSR primers	Produced 52 bands with 51.9% polymorphism; primer polymorphism reached 71.43%; ISSR clustering agreed with morpho-chemical traits	Genetic diversity assessment and landrace characterization	(45)
30 off-season Kerala accessions	10 ISSR + 20 SSR primers	ISSR polymorphism of 65.3%; PIC 0.02–0.29; expected heterozygosity 0.183;	Population genetics, elite accession	(44)

		resolved district-wise genetic structure and identified low-glycaemic-index accession KNR-1	identification and breeding	
Polyphenol-rich jackfruit leaves	Optimized ISSR amplification protocol	Improved DNA quality and amplification reproducibility using modified CTAB extraction and ISSR primer TC10G	Molecular characterization protocol optimization	(46)

3.4 SNP Markers and Next-Generation Sequencing Approaches

Molecular characterization of jackfruit (*Artocarpus heterophyllus* Lam.) has progressed from conventional PCR-based markers to genome-wide approaches enabled by next-generation sequencing (NGS). One study (10) reported a draft genome of ~982 Mb and 35,858 annotated genes, which is the first whole genome resource and serves as an important reference for SNPs, comparative genomics and gene annotation. On this foundation, a subsequent study (11) sequenced the year-round Bangladeshi cultivar BARI Kanthal-3 and created an important genomic resource for study of flowering behaviour and other agronomic traits, with a 1.62% heterozygosity and an estimated 16 million SNPs, of which close to 90% were located in intergenic regions.

A further study (12) then sequenced 295 accessions from South and Southeast Asia with the reference genome (986 Mb) and uncovered over 95 million SNPs and population structure signals of several domestication and introduction events. These studies illustrate the level of detail gained from the genetic diversity analysis of NGS-enabled SNP resources, for domestication studies, discovery and selection of candidate genes, and molecular breeding. However, the genome-wide investigations are still limited in the jackfruit with extensive germplasm collections from India, Sri Lanka and Bangladesh to be explored, which will help to speed up conservation and precision breeding in jackfruit.

4. Biochemical Characterization of Jackfruit Germplasm

Biochemical characterization is complementary to DNA-based profiling as it reflects metabolic and compositional differences that are final determinants of fruit quality, nutritional value and end use. In the South Asian and comparative international literature, five major biochemical aspects of the variability of jackfruit germplasm have been explored: (i) proximate nutritional composition, (ii) phytochemical and antioxidant diversity, (iii) protein, isozyme and enzyme-based variation, (iv) starch and carbohydrate architecture, and (v) lipid and volatile/aroma composition. This section is not a simple summary of the descriptive traits reported across individual studies. Rather, it synthesises studies in which methodologies and reported values have varied, to establish where genuine diversity, as opposed to methodological noise, has been substantiated at least at the accession level.

4.1 Nutritional Composition and Macronutrient Diversity

Jackfruit pulp has been consistently reported as moisture rich, high in carbohydrates, poor in protein and fat, but the range of variation reported among studies is wide enough to suggest that these differences stem not only from analytical variation but also from cultivar and developmental disparities. Proximate analysis of ripe pulp has representative values of moisture 77%, carbohydrate 18.9 g/100 g, protein 1.9 g/100 g, fat 0.1 g/100 g, crude fibre 1.1 g/100 g and energy value 84–95 kcal/100 g (47). The range reported by independent reviews is similar, but not equivalent, due to differences in ripening stage, cultivars and analytical procedures for the primary studies that they draw on (48, 49). The vitamin C content is consistently reported as nutritionally significant, ranging from 13 to 14 mg/100 g in various sources (47), but with large inter-accession variation reported in others in the literature reviewed here.

A germplasm survey conducted in the field is the best and most unequivocal proof that these characteristics are genetically variable, and not merely methodologically. A study conducted on jackfruit genotypes in Pudukkottai district, Tamil Nadu revealed that the genotype-to-genotype variations (CV%) of various biochemical parameters such as total soluble solids, total sugars, reducing and non-reducing sugars, titratable acidity, ascorbic acid and carotene content were observed to vary significantly ranging from 10.01% to 41.86% and 16.22% to 32.81% respectively (50). Likewise, a chemical composition study on jackfruit selections from Western Ghats of India, the main centre of diversity of the species, revealed significant variation in the total soluble solids, titratable acidity, sugars, starch and carotenoid content among the genotypes, with the total soluble solid content ranging from about 15 to more than 40 °Brix across the accessions reported in the broader literature included in this study (51). Both germplasm surveys independently arrive at the same conclusions: sugar, acid and carotenoid traits have the greatest discriminating power with regard to the characterization of jackfruit accessions, whereas carotenoid content in particular exhibits disproportionately high variability compared to other proximate traits and is therefore an interesting target trait for biochemical–molecular marker association work. Representative nutritional composition values for ripe jackfruit pulp are summarised in Table 5.

Table 5. Nutritional composition of ripe jackfruit pulp

Parameter	Unit	Reported value/range	Source(s)
Moisture	%	≈77 (representative value, ripe pulp)	(47)
Carbohydrate	g/100g FW	≈18.9	(47)
Crude protein	g/100g FW	≈1.9	(47)
Crude fat	g/100g FW	≈0.1	(47)
Crude fibre	g/100g FW	≈1.1	(47)

Energy	kcal/100g	84–95	(47)
Vitamin C	mg/100g FW	≈13–14	(47)
Total soluble solids (TSS)	°Brix	Wide inter-accession range (genotype survey)	(51)
Titratable acidity	%	Genotype-dependent; low overall (~0.13% as citric acid at ripe stage in reference genotype)	(51)
Ascorbic acid	—	High inter-genotype variability (CV = 32.81%)	(50)
Carotene / carotenoid content	—	Highest inter-genotype variability among traits assessed (CV = 41.86%)	(50)(51)

4.2 Phytochemical Diversity and Antioxidant Properties

A common trend across the literature reviewed was that the in vitro antioxidant activity, and hence the level of phenolics and flavonoids, of non-pulp tissues (seed, leaf, peel/rind and the fibrous "tegmen" seed coat) was generally significantly higher than of ripe pulp. Polyphenol rich crude extracts with demonstrated free-radical scavenging and anti-proliferative activity were reported in a targeted study of the seed coat (tegmen) (52), and pectin extracted from the slimy sheath of the seed also showed measurable phenolic content and antioxidant activity, determined using DPPH, FRAP and CUPRAC assays (53). Ripened pulp extracts were screened using DPPH assays in four different solvent systems, acetone, aqueous, ethyl-acetate/methanol and ethyl-acetate, which revealed that extraction solvent had a significant effect on measured antioxidant activity, and the acetone extracted sample exhibited the highest number of flavonoids recovered and the highest radical-scavenging activity of the four solvents tested (54). The solvent dependency is a common methodological confounding factor across the phytochemical literature and a fact that makes it difficult to compare total phenolic/flavonoid values from different studies unless the studies are standardized in terms of extraction protocol (see below, Section 4.7 for explicit mention).

Similar tissue gradients were observed in the germplasm of all jackfruit tissues (seed, peel and leaf) not utilized for consumption in Kenya, with extracts of the tissues rich in phenolics exhibiting significant antioxidant and antimicrobial activities, as well as unique mineral composition (55). Similarly, RAPD-based screening of leaf-tissue accessions has also shown that there are accession-specific phytochemically distinct genotypes that can be identified by combining qualitative phytochemical screening with molecular banding patterns, thus highlighting accession-specific phytochemical variability and not the uniformity of germplasm (39). As highlighted in Section 4.1, carotenoid content is highly variable at a level of accessions and is the most common pigment class that is associated with the variation in pulp colour from

All evidence points to three conclusions: (i) seeds, leaves and tegmen tissues are a significantly under-exploited phytochemical resource compared with pulp; (ii) differences in accession-level antioxidant/phenolic content are real and have been shown in several independent panels of germplasm; (iii) despite a relatively high number of antioxidant/phenolic values reported across the literature, the values reported are complicated by the lack of standardisation of extraction and assay protocols, and therefore cannot be directly compared quantitatively across studies as much as they can be qualitatively compared for trends.

4.3 Protein, Isozyme and Enzyme-Based Characterization

The biochemical approaches relevant to germplasm characterization include isozyme electrophoresis and the characterization of seed storage proteins. Isozyme analysis represents one of the earliest biochemical methods used to assess jackfruit diversity. Using four enzyme systems—alcohol dehydrogenase (ADH), glutamate oxaloacetate transaminase (GOT), malate dehydrogenase (MDH), and acid phosphatase (ACP)—Azad et al. (6) identified 19 electrophoretic banding patterns and 31 isozyme phenotypes among 50 accessions. The observed diversity closely corresponded with morphological and agroecological variation, demonstrating the usefulness of isozymes as complementary genetic markers for germplasm characterization.

Recent studies have shifted attention toward seed storage proteins because of their nutritional and industrial potential. Comprehensive structural (FTIR, DSC, TGA, SEM, and XRD) and functional analyses have demonstrated that jackfruit seed protein isolates possess desirable solubility, emulsifying, foaming, and water- and oil-binding properties, supporting their use as functional food ingredients (56). Microwave-assisted extraction has further improved protein solubility and altered protein microstructure compared with conventional extraction methods (57). Similar protein characterization has also been reported for jackfruit leaves (58). In addition, the seed lectins jacalin and artocarpin have attracted considerable interest because of their biological activities and potential value as chemotaxonomic markers within the genus Artocarpus, although this application remains insufficiently validated across diverse germplasm collections (47, 59). Isozyme systems and seed-protein characteristics reported across studies are summarised in Table 6.

Table 6. Isozyme systems and seed-protein characteristics reported in jackfruit germplasm

System / Protein	Tissue	Method / Finding	Significance	Reference
Alcohol dehydrogenase (ADH)	Seedling tissue (50 accessions)	1–5 bands per pattern; part of 4-enzyme isozyme panel	Confirmed morphological diversity patterns; least diversity in saline-belt accessions	(6)
Glutamate	Seedling	Component of 19 combined	Co-dominant biochemical	(6)

oxaloacetate transaminase (GOT)	tissue	electrophoretic patterns / 31 isozyme phenotypes	marker complementing morphology	
Malate dehydrogenase (MDH)	Seedling tissue	1–3 bands	Contributes to overall isozyme phenotype diversity	(6)
Acid phosphatase (ACP)	Seedling tissue	Component of isozyme panel	Completes the 4-system isozyme panel used for diversity confirmation	(6)
Jacalin (seed lectin)	Seed	Reported to represent a very large proportion of total seed protein; binds human IgA and T-antigen	Proposed chemotaxonomic marker at genus level; not yet systematically tested across South Asian germplasm panels	(47); (59)
Artocarpin (seed lectin)	Seed	Broader monosaccharide reactivity than jacalin	Co-occurs with jacalin; taxonomic marker candidate	(47)
Seed protein isolate (structural/functional)	Seed	Characterized by FTIR, DSC, TGA, SEM, XRD; solubility, water/oil binding, emulsifying and foaming properties profiled	Establishes seed protein as a technofunctional ingredient, not only a nutritional trait	(56)
Seed protein — extraction-method comparison	Seed	Protein solubility 81.48% (microwave-assisted) vs. 79.48% (acid–alkali precipitation)	Extraction method measurably changes functional protein quality; a methodological, not purely genetic, source of variation	(57)
Leaf protein concentrate	Leaf	Amino acid profile, functional properties and thermal behaviour characterized	Extends protein characterization beyond seed tissue	(58)

4.4 Starch and Carbohydrate Characterization

Starch is a quantitatively important and functionally unique component of jackfruit in that it combines high amylose content with a distinctive granule architecture, giving it functional properties, such as elevated gelatinization temperature and slow digestibility, that are uncommon among conventional cereal and tuber starches, especially in its seed, and has become a functional trait of increasing importance as a jackfruit character trait. The amylose content of jackfruit starch has been consistently reported to be high, with values ranging from approximately 22.10% to 38.34% across different studies compiled in a dedicated compositional and functional review (60), which are higher than the amylose content reported by most of the other common cereal and tuber starches used for comparison in the same review. This is an interesting high-amylose characteristic of jackfruit starch because it is linked to an increased gelatinization temperature and decreased starch digestibility with limited swelling of the granules when cooked, which makes the jackfruit starch a potential source for resistant/slowly digestible starch fractions for functional-food applications (60). Beyond the functional quality relevance of starch architecture, it has been reported that there is also accession-level diversity signal with regard to starch architecture, as starch size and shape (round, bell-shaped and semi-oval) differ severalfold between accessions across various cultivars (60). The methods of extraction (wet-grinding, alkaline, enzymatic or surfactant-assisted) will also affect the measurement of starch yield and purity; comparisons of starch traits between different studies should be interpreted with the caveats generally recommended for phytochemical data in Section 4.2. Starch composition and functional characteristics reported across studies are summarised in Table 7.

Table 7. Starch composition and functional characteristics of jackfruit starch

Trait	Reported value / finding	Functional implication	Reference
Amylose content	22.10–38.34% (compiled across studies/origins)	Classified as a high-amylose starch relative to common cereal/tuber references	(60)
Gelatinization temperature	Elevated relative to lower-amylose starches	Restricted granule swelling; relevant to processing behaviour	(60)
Digestibility	Comparatively low	Positions jackfruit (especially seed) starch as a candidate resistant/slow-digestible starch source	(60)
Granule morphology	Round, bell-shaped or semi-oval depending on cultivar/origin; size differs severalfold between accessions	Accession-level diversity signal independent of amylose content	(60)
Extraction-	Wet-grinding, alkaline, enzymatic and	Cross-study comparisons require matched	(60)

method sensitivity	surfactant-assisted methods give different yield/purity	extraction protocol	

4.5 Composition of Lipids and Fatty Acids

Jackfruit seed oil is characterized by a predominantly unsaturated lipid profile, although the reported fatty acid composition varies among studies. Gas chromatographic analysis of seed oil from six geographical regions identified palmitic acid (39.9%) and linoleic acid (30.2%) as the predominant fatty acids, with total saturated and unsaturated fatty acids accounting for 45.6% and 52.9%, respectively. Omega-3 fatty acids, primarily linolenic acid and eicosapentaenoic acid, constituted approximately 9.9% of the total fatty acid profile (61) Eicosapentaenoic acid (EPA) is a long-chain omega-3 fatty acid typically associated with marine, rather than plant, lipid sources, so this reported value warrants cautious interpretation and verification against the original analytical method before being generalized across jackfruit germplasm. While no significant variation was observed among geographical origins, post-harvest processing (fresh, dried, or boiled seeds) significantly altered the concentration of unsaturated fatty acids, indicating that processing can influence lipid composition as much as germplasm origin. In addition, Nagala et al. (62) combined gas chromatographic fatty acid profiling with antioxidant assays (DPPH and FRAP), highlighting the value of integrating compositional and functional analyses for seed oil quality assessment. The variability reported across studies emphasizes the need for standardized analytical protocols to facilitate reliable comparisons of lipid composition among jackfruit germplasm. Fatty acid composition of jackfruit seed oil across studies is summarised in Table 8.

Table 8. Fatty acid composition of jackfruit seed oil and major aroma-active volatile compounds

Compound / Class	Reported value	Tissue / Source	Notes	Reference
Palmitic acid (C16:0)	≈39.9% of total FA (highest single FA)	Seed oil	Dominant saturated FA; six-region survey, no significant regional variation	(61)
Linoleic acid (C18:2, ω-6)	≈30.2% of total FA	Seed oil	Dominant unsaturated FA	(61)
Total saturated FA	≈45.6%	Seed oil	Sum of saturated fraction	(61)
Total unsaturated FA (MUFA+PUFA)	≈52.9%	Seed oil	Sum of mono- + polyunsaturated fraction	(61)
Total omega-3 PUFA	≈9.9%	Seed oil	Linolenic + eicosapentaenoic-type acids; below GC detection limit in some processed (boiled/dried) seed	(61)
Ethyl 3-methylbutanoate	Highest OAV (≈74,000) and highest FD factor of all volatiles assayed	Ripe pulp	Single most odour-active compound identified by AEDA/OAV	(63)
Ethyl butanoate	OAV ≈1,800; FD factor 256	Ripe pulp	Second most odour-active ester	(63)
3-Methylbutanal / 2-methylpropanal	OAV 1,500 / 1,400	Ripe pulp	Major aldehyde contributors to fresh, malty notes	(63)
Butyl butanoate / butyl 3-methylbutanoate	FD factor 128 (each)	Ripe pulp	Secondary fruity-note contributors	(63)

4.6 Volatile Compounds and Aroma Profiling

The characteristic aroma of jackfruit results from a complex mixture of volatile esters, aldehydes, and alcohols. Recent aroma-chemistry studies have provided more precise characterization than earlier compositional GC–MS surveys by incorporating sensory validation. Using aroma extract dilution analysis (AEDA) and odour activity value (OAV) calculations, Grimm and Steinhaus (63) identified ethyl 3-methylbutanoate as the predominant aroma-active compound in ripe jackfruit pulp, with ethyl butanoate, 3-methylbutanal, and 2-methylpropanal also contributing significantly to the characteristic flavour. These findings provide a more reliable assessment of aroma quality than earlier GC–MS studies based solely on volatile composition (64). More recently, integrated multi-omics analyses have linked differences in volatile metabolites between jackfruit varieties to their underlying metabolic and genetic variation, providing new insights into the molecular basis of aroma (65). Collectively, these advances highlight the transition from descriptive volatile profiling to functionally validated aroma characterization, strengthening its application in germplasm evaluation and quality improvement.

4.7 Synthesis: Trends, Inconsistencies and Research Gaps

Three major trends emerge from the literature. First, most biochemical studies have focused on fruit pulp, whereas seeds, leaves, and the tegmen often exhibit higher concentrations of phenolics, proteins, and, in seeds, starch, indicating that a substantial portion of jackfruit biochemical diversity remains underexplored. Second, methodological heterogeneity including differences in molecular markers, extraction protocols, and analytical techniques limits direct quantitative

comparisons among studies, making reported values more representative than directly comparable. Third, studies evaluating multiple accessions using standardized methods consistently reveal considerable accession-level variation in carotenoids, sugars, organic acids, and other quality traits, highlighting their potential for germplasm selection and breeding.

Several research gaps remain. Untargeted metabolomic profiling (LC–MS and GC–MS) has rarely been applied to well-defined germplasm panels, and few studies have integrated biochemical traits with SSR or SNP-based molecular datasets beyond the isozyme–morphology concordance reported by Azad et al. (6). In addition, the use of isozyme and protein electrophoresis has declined markedly despite their value as complementary diversity markers. Finally, the absence of standardized analytical protocols across multi-country germplasm collections limits the establishment of reliable regional reference values for biochemical traits.

5. Integration of Molecular and Biochemical Data for Germplasm Characterization

Sections 3 and 4 demonstrate that molecular markers and biochemical profiling independently capture substantial diversity within jackfruit germplasm. However, relatively few studies have integrated these complementary datasets to provide a comprehensive understanding of genotype–phenotype relationships. An early example is the study by Azad et al. (6), in which morphological, agroecological, and isozyme analyses produced concordant patterns of germplasm diversity, illustrating the value of integrating independent datasets.

Despite this evidence, integrated characterization remains uncommon. Most molecular studies using RAPD, ISSR, SSR, or SNP markers have focused primarily on genetic diversity, whereas biochemical investigations have generally been conducted without corresponding molecular analyses on the same accession panels. Consequently, formal statistical integration using approaches such as principal coordinate analysis, Mantel tests, or hierarchical clustering has rarely been applied. Notable exceptions include the comparative molecular–phytochemical analysis by Prasad et al. (39) and the integration of SSR, biochemical, and geo-referenced diversity data for conservation prioritization by Gurjar et al. (66).

Integrating molecular and biochemical characterization is essential because each approach provides complementary information. Molecular markers reveal genetic relationships and population structure, whereas biochemical analyses quantify nutritional and quality-related traits. Combining these datasets within well-characterized germplasm panels would enable robust marker–trait association studies, strengthen conservation strategies, and accelerate marker-assisted breeding. Establishing standardized accession panels with integrated genomic and biochemical datasets should therefore be a priority for future jackfruit research.

6. The Use of Molecular and Biochemical Characterization in Germplasm Management

Molecular and biochemical characterization provide essential tools for germplasm management, conservation, and breeding. Three major applications are supported by the available literature. First, molecular markers such as RAPD, ISSR, and SSR facilitate the identification of duplicate accessions, enabling the rationalization of field genebanks while maintaining genetic diversity and reducing conservation costs (27). Second, characterization data support the development of core collections that capture maximum genetic diversity with a manageable number of accessions. The Indian Agricultural Research Institute has established a jackfruit core collection, whereas similar national collections remain limited in other jackfruit-growing regions, highlighting disparities in germplasm management (67). Third, integrating molecular, biochemical, and geo-referenced diversity data provides a robust framework for conservation prioritization by identifying genetically distinct and nutritionally valuable germplasm (66).

Advanced applications, including marker-assisted breeding, genomic selection, transcriptome-assisted breeding, and marker–trait association studies, remain largely unexplored in jackfruit. Although chromosome-scale reference genomes and genome-wide SNP resources are now available (10, 12, 11), their successful application will require well-phenotyped germplasm panels and integrated molecular–biochemical datasets to accelerate conservation and genetic improvement.

7. Impacts of Germplasm Conservation and Breeding

7.1 Ex Situ Conservation

The pattern of ex situ conservation of tropical fruit tree genetic resources in general (68) is reflected in the ex-situ conservation of jackfruit genetic resources, which is predominantly through field genebanks maintained by national agricultural research systems in South Asia. Molecular characterization is directly used to support this conservation infrastructure, and is used to identify duplicate accessions, verify the genetic identity of germplasm during transfer between institutions, and confirm clonal fidelity in vegetatively propagated material (42). Given that jackfruit is a large, long generation tree crop, ensuring the survival of field genebanks is a very costly process in comparison to seed banked staple crops which further strengthens the argument for molecular-marker based redundancy screening as a cost management tool.

7.2 Core Collection Development

Core collections aim to represent the genetic diversity found in a larger germplasm assemblage, but to minimize the number of accessions that need to be routinely maintained and tested. As mentioned in Section 6, Indian Agricultural Research Institute has developed a jackfruit core collection based on this principle and similar national-level core collections do not exist, except in Uganda where they are currently being established at the Gwokyalya site (67). This indicates that core-collection work has already progressed further in the primary centre of diversity (the South Asian countries) than in secondary centres such as East Africa and Southeast Asia, where equivalent collections have yet to be established.

7.3 Molecular-Assisted Breeding

Molecular characterization data are used indirectly for breeding at present, mostly for parentage verification, clonal fidelity tests and identification of genetically distinct elite accessions that could be used as breeding parents (42, 35). Direct marker-assisted selection for specific quality or agronomic traits (typical of many field and horticultural crops) has not been reported in the jackfruit literature surveyed here, which is not surprising because marker-trait association studies have yet to be conducted (Section 6). Technical support for this work comes from the genomic resources outlined in Section 3.4; the missing element is not markers but populations of sufficient size with markers that can be phenotyped and used to detect associations with confidence.

8. Challenges and Research Gaps

Four major challenges emerge from the literature reviewed. First, methodological heterogeneity remains a significant limitation. Variations in molecular marker systems, primer sets, extraction protocols, and analytical methods hinder direct quantitative comparisons of genetic and biochemical data across studies. Second, geographic coverage is uneven, with most studies originating from India, while germplasm from several jackfruit-growing regions remains underrepresented. Third, integrated characterization using molecular and biochemical data from common accession panels is still uncommon, limiting the identification of robust marker–trait associations and their application in breeding. Fourth, although isozyme and protein electrophoresis have historically served as cost-effective diversity markers, their application has declined considerably since the 1990s, despite their potential value as complementary tools alongside modern SNP-based approaches (6).

These challenges represent limitations of the literature evaluated in this review rather than the entire body of published research. For example, germplasm from Southeast Asia and the Philippines remains largely uncharacterized relative to South Asian collections (Section 3), and few studies pair a common accession panel with both molecular markers and biochemical assays (Section 5), which is precisely the kind of standardized, multi-site phenotyping gap identified above. Addressing them through standardized methodologies, broader germplasm sampling, integrated molecular–biochemical analyses, and multidisciplinary approaches will improve the reliability of germplasm characterization and enhance conservation and breeding efforts.

9. Future Perspectives

Future research on jackfruit germplasm characterization should focus on five key priorities. First, genome-scale characterization should be expanded to geographically representative germplasm panels to improve analyses of genetic diversity, population structure, and domestication. Second, well-phenotyped accession panels are needed to enable robust marker–trait association studies for economically important traits such as carotenoid content, sugar and acid composition, fruit quality, and seed nutritional attributes. Because traits such as sugar and carotenoid content are also strongly influenced by environmental conditions, multi-location or multi-season trials should be incorporated to distinguish genetic from environmental sources of variation before marker–trait associations are validated for breeding use. Third, untargeted metabolomic approaches, including LC–MS and GC–MS, should complement conventional biochemical analyses to provide comprehensive biochemical characterization and identify biomarkers associated with nutritional quality and stress tolerance (69, 70). Fourth, molecular, biochemical, phenotypic, and geo-referenced data should be generated from the same germplasm panels using standardized protocols to strengthen marker–trait discovery, germplasm classification, and marker-assisted breeding. Finally, nationally and regionally coordinated core collections should be expanded beyond India, particularly in East Africa and Southeast Asia, to improve conservation efficiency and facilitate international germplasm exchange (67).

The integration of genomics, metabolomics, high-throughput phenotyping, bioinformatics, and artificial intelligence offers new opportunities for comprehensive germplasm characterization. Adopting multidisciplinary and standardized approaches will strengthen conservation strategies, accelerate breeding programmes, and promote the sustainable utilization of jackfruit genetic resources.

10. CONCLUSION

Over the past three decades, jackfruit germplasm characterization has progressed from reliance on morphological descriptors to the application of advanced molecular markers and comprehensive biochemical profiling. The literature reviewed demonstrates that jackfruit possesses substantial genetic and biochemical diversity, particularly within its primary centre of diversity in South Asia, providing a strong foundation for conservation and crop improvement. Despite these advances, molecular and biochemical characterization have largely evolved as parallel research approaches, with relatively few studies integrating both datasets using common germplasm panels; this fragmentation remains the central limitation of the field. Consequently, opportunities to identify robust marker–trait associations and translate genomic information into breeding programmes remain limited. The recent availability of chromosome-scale reference genomes and genome-wide SNP resources has largely overcome previous technical constraints, shifting the primary challenge toward developing standardized, well-phenotyped, and geographically representative germplasm collections that can be screened with these genomic resources. Translating this potential into practical breeding gains will require nationally and regionally coordinated core collections, common accession panels phenotyped under standardized, multi-environment protocols, and the routine pairing of genomic data with biochemical and morphological datasets. Future progress will depend on integrating molecular, biochemical, phenotypic, and geo-referenced data within unified analytical frameworks. Such multidisciplinary approaches will improve germplasm conservation, strengthen marker-assisted breeding, and

accelerate the development of nutritionally superior, climate-resilient, and high-yielding jackfruit cultivars, thereby maximizing the sustainable utilization of this underexploited tropical fruit crop.

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Author Contributions
The review was conceived by MR. MR conducted the literature search, compiled and analysed the published literature, prepared the figures and tables, and wrote the first draft of the manuscript. VSKS provided critical revisions, supervised the work, and contributed to the interpretation and organization of the review. AJ, MBN, and BA reviewed, revised, and approved the final version of the manuscript.

Data Availability
Data sharing does not apply to this article because no new datasets were generated or analysed during the current study. All information presented in this review was obtained from previously published sources, which are appropriately cited in the manuscript.

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