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# JACKFRUIT (ATROCARPUS HETEROPHYLLUS LAM.) AS A SUSTAINABLE FOOD RESOURCE: ZERO-WASTE VALORIZATION, VALUE ADDITION, FUNCTIONAL FOOD DEVELOPMENT, AND THE EMERGING ROLE OF CRISPR-CAS GENOME EDITING IN OVERCOMING FUNGAL DISEASES – REVIEW

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**ABSTRACT:**
Jackfruit (Artocarpus heterophyllus Lam.) is a large, underutilized tropical fruit crop with substantial potential to contribute to sustainable food security, circular bioeconomy development, and functional-food innovation. The fruit is nutritionally valuable, providing starch, dietary fibre, resistant starch, protein, minerals, and diverse phenolic phytochemicals. However, approximately 50-70% of fruit mass may be discarded during processing, creating an environmental burden while simultaneously representing a substantial opportunity for biorefinery based valorisation. This review examines the nutritional and functional food properties of jackfruit and evaluates the potential of its processing by-products, including jackfruit flour, starch, pectin, bioactive extracts, biochar, bioethanol, and biodegradable packaging materials, for the development of zero-waste value chains. The major biotic constraints limiting jackfruit productivity are also reviewed, with particular emphasis on fungal diseases such as Rhizopus fruit rot, anthracnose, and dieback, which can collectively contribute to substantial pre-harvest losses, with Rhizopus fruit rot alone reported to cause losses of approximately 15–32% in affected orchards.
The review then explores CRISPR–Cas9 genome editing and its emerging derivatives, including base editing, prime editing, and CRISPR activation, as precision approaches for developing durable disease resistance in jackfruit. Validated examples from related tropical and subtropical crops, including banana, citrus, cassava, and cacao, as well as major crops such as wheat and tomato, demonstrate the potential of genome editing to target susceptibility (S) genes and defence-related pathways and to generate resistance to fungal and fungal-like pathogens. The availability of draft jackfruit genome sequences now provides an important foundation for identifying homologous targets and developing a precision-breeding framework for disease resistance. However, successful implementation will require advances in jackfruit-specific tissue culture and regeneration systems, functional validation of candidate genes, delivery technologies, field evaluation, and careful consideration of regulatory, ethical, and socioeconomic factors. Overall, the evidence reviewed supports an integrated strategy combining genome-edited disease resistance with zero-waste circular valorisation and improved post-harvest management as a promising pathway for transforming jackfruit into a more sustainable, economically viable, and climate-resilient food crop.

**KEYWORDS:** jackfruit; Artocarpus heterophyllus; zero-waste valorization; functional food; CRISPR-Cas9; genome editing

## INTRODUCTION

The challenges on the global food system are unprecedented, including the increasing demand of more food and less available land, climate changes, and the continued losses of pre- and post-harvest factors (1,2). In this context, there is renewed scientific and policy interest in "orphan" and "underutilized" crops that have a high nutritional value, resilience and low input needs, in addition to the few staple crops that currently feed the world. One of such crops is jackfruit (Artocarpus heterophyllus Lam.) which is also the national fruit of Bangladesh (3,4). Jackfruit is a tree fruit of the Western Ghats of India, which is cultivated throughout South and Southeast Asia, Africa and some parts of Latin America, and is known for its largest tree borne fruit, reaching 30-50 kg in weight (3).
Jackfruit has a number of important nutritional uses, such as a plant-based meat alternative in Western markets, both in its unripe (green) and ripe state due to its low-glycemic index or processed into various products

including chips, jams, nectar and snacks after dehydration (3,4). The jackfruit seeds, rind, rag (perianth) and latex are an enormous untapped source of starch, dietary fibre, protein and bioactive phytochemicals (1,5,6). Half to two-thirds of the jackfruit weight is lost during processing, which can lead to environmental pollution if not managed properly, but can also be utilized as value-added ingredients, nutraceuticals, bioenergy feedstocks and biodegradable packaging materials in the context of a zero-waste circular bioeconomy (1,2,65). Jackfruit is still considered as an "orphan crop" in most producing countries, being underexploited in the market. The trees and fruits are easily vulnerable to biotic stress, especially fungal diseases viz., Rhizopus fungus rot (Rhizopus stolonifer, syn. Rhizopus artocarpi), anthracnose (Colletotrichum spp.) and dieback (Lasiodiplodia theobromae). Pre-harvest fruit losses due to these pathogens range from 15–32% under favourable climatic conditions, and no jackfruit cultivar is currently known to possess genetic resistance to these pathogens (7-9,11,12). The lack of durable resistance in jackfruit represents a significant agronomic and economic constraint, further limiting its potential as a climate-resilient food-security crop. This concern is particularly important because fungi and oomycetes are responsible for a substantial proportion of crop losses, accounting for up to 20% of pre-harvest losses and an additional 10% of post-harvest losses across major food crops. (13-17).

Traditional approaches to managing fungal diseases, including cultural sanitation, pruning to improve canopy ventilation, and the application of copper- or triazole-based fungicides, often provide limited and non-durable protection while raising environmental and food-safety concerns (11,12). Although some disease-resistant jackfruit germplasm has been characterized, the limited availability of resistant germplasm, combined with the long juvenile period and high heterozygosity of jackfruit, presents substantial challenges for conventional breeding for disease resistance (3,63,64).

The advent of CRISPR–Cas genome-editing technology offers a potentially transformative opportunity in this context, owing to its relative speed, efficiency, and precision in engineering disease resistance in plants. Over the past decade, heritable resistance to fungal pathogens has been successfully developed in staple and horticultural crops using CRISPR-Cas9 and its derivatives, including base editing, prime editing, and CRISPR activation. Many of these strategies target susceptibility (S) genes-host genes that are exploited by pathogens to facilitate infection. Notably, heritable resistance to powdery mildew has been achieved in wheat, tomato, and grapevine through targeted modification of the MLO locus, while resistance to citrus canker has been developed by editing the promoter region of LOB1 (18-24). With the recent availability of a draft jackfruit genome sequence (63,64), it is now technically feasible to identify jackfruit orthologues of validated S genes and other defence-associated genes. This provides a foundation for developing genome-edited jackfruit cultivars with enhanced disease resistance, potentially without introducing foreign DNA and thereby distinguishing such plants from conventional transgenic organisms.

The three main aims of this review are as follows. First, we provide an overview of the available evidence on the nutritional composition and functional-food potential of jackfruit and its by-products. Second, we examine zero-waste valorisation strategies for converting jackfruit processing residues into value-added food, packaging, energy, and pharmaceutical products, thereby positioning jackfruit within a circular bioeconomy framework. Third, and most importantly, we provide a detailed assessment of the fungal diseases that constrain jackfruit production and, through case studies of analogous fruit and cereal crops, explore how genome-editing technologies, particularly CRISPR–Cas, could be strategically employed to develop durable fungal disease resistance in jackfruit.

## 2. Botanical Overview, Global Distribution and Economic Importance of Jackfruit

Artocarpus heterophyllus Lam. is an evergreen tree in the Moraceae family, closely related to breadfruit, A. altilis and mulberry, Morus spp. (63). The tree is monoecious with separate male and female inflorescences on the same plant; the edible "fruit" is actually a multiple fruit (syncarp) in which numerous individual flowers each develop a fleshy perianth (the edible bulb or "rag"), surrounded by a single seed (3,9). The jackfruit tree can produce for decades and the fruit is 5–50kg in weight depending on cultivar and growing conditions (3).

Jackfruit originated in the tropical rainforests of the Western Ghats of India and has since spread across South and Southeast Asia, East Africa, and more recently to North America and Australia (3,4). It is an important fruit crop in India, Bangladesh, Thailand, Indonesia, Sri Lanka, Malaysia, and Vietnam, with Bangladesh officially recognizing jackfruit as its national fruit (4). Despite its wide geographic distribution and cultural importance, jackfruit remains a relatively low-volume commodity compared with major fruit crops such as banana, mango, and citrus. Production is predominantly undertaken by smallholder farmers and homestead growers rather than in large-scale commercial orchards (3,4).

Several factors support the economic and strategic case for expanding jackfruit cultivation and processing. First, jackfruit trees are relatively tolerant to marginal soils, drought, and heat stress compared with many commercial fruit crops, making them a promising crop for climate-change adaptation (3). Second, some varieties and cultivars exhibit extended or nearly year-round fruiting. Its extended production period, could broaden the harvesting and processing window and contribute to greater income stability for smallholder farmers (64). Third, growing global demand for plant-based foods has created new commercial markets for young/green jackfruit as a meat analogue in packaged foods and restaurant products, particularly in North America, Europe, and Australia (3,4). Together, these trends strengthen the strategic case for investment in jackfruit value addition and disease-resistance breeding, which are the central themes of this review.

## 3. Nutritional Composition and Functional Food Potential of Jackfruit

### 3.1 Composition of the Edible pulp

The ripe perianth of the jackfruit is a low fat, high fibre, nutritionally dense food, with a balanced micronutrient profile, and is rich in vitamin C, vitamin A, thiamine, riboflavin, niacin, folate, potassium, magnesium, manganese and calcium (3,4). Phytochemically, jackfruit pulp harbours a good stock of flavonoids, tannins and other phenolic acids, volatile organic acids, free amino acids and carotenoids, the levels of which change depending on the ripening stage, cultivar and conditions under which it is grown (3).

### 3.2 Jackfruit Seeds: An Underexploited Functional Ingredient

Jackfruit seeds, which account for approximately 10–15% of the total fruit weight, are generally regarded as processing waste despite possessing a nutrient profile comparable to, and in some respects superior to, that of several cereal grains (4,5,7,8). Analytical studies indicate that jackfruit seed flour contains approximately 12.9–17.9 g/100 g starch, around 18% protein, and 1.6–3.9 g/100 g dietary fibre. It is also a notable source of resistant starch (19.9–25.6 g/100 g in some studies) and amylose (5,7). In addition, jackfruit seeds contain essential minerals, including magnesium, potassium, phosphorus, sodium, calcium, copper, manganese, iron, and zinc, as well as bioactive phenolic compounds such as catechin, ferulic acid, epicatechin, rutin, and gallic acid (4,5). Preclinical studies have associated these bioactive constituents with antioxidant, antidiabetic, anticancer, hepatoprotective, antimicrobial, and anti-inflammatory activities, highlighting the potential of jackfruit seeds as functional food ingredients and sources of nutraceutical compounds rather than simply as waste materials (4,5,7,8,10).

The reported functional applications of jackfruit seed flour and starch include their incorporation into bakery products, pasta, and extruded snacks; enrichment of fermented dairy products such as yogurt with additional protein and minerals; and development of resistant-starch-based food ingredients for glycemic management (3,7). Particularly promising is their application as wall materials for the microencapsulation of labile bioactive compounds such as β-carotene. Jackfruit seed starch matrices have demonstrated greater protection of encapsulated carotenoids during simulated gastrointestinal digestion than commercial potato starch (3,7). Furthermore, the polyphenol rich fraction of green jackfruit flour has been reported to inhibit α-glucosidase, α-amylase, aldose reductase, and non-enzymatic glycation-biochemical processes associated with diabetes-further supporting the potential incorporation of jackfruit-derived ingredients into the expanding functional-food and nutraceutical sectors (10,67).

### 3.3 Rind, Rag and Latex: Additional Functional Fractions

The rind (peel) and the rag of jackfruit contains other carbohydrate polymers and phenolic antioxidants, which are discussed in Section 4, and have applications downstream the food and non-food sector. The latex exuded from the jackfruit plants is a viscous substance and has been used in traditional medicine, as a natural adhesive, as a cementing agent, and in dental restorative formulations, but its allergic properties in sensitized people should not be neglected when used in food-grade preparations (2).

### 3.4 Functional Food & Nutraceutical Positioning

The compositional data compiled in Table 1 collectively support the classification of jackfruit as a multifunctional food resource. The pulp, seeds, and rind have considerable potential as sources of dietary fibre, resistant starch, plant protein, and diverse phenolic antioxidants for human nutrition. This composition aligns well with current trends in functional-food development, particularly in the areas of gut health, owing to the presence of prebiotic fibre and resistant starch (3-5); metabolic health, through phytochemicals with antioxidant and antidiabetic properties (10,44); and plant-protein diversification (3-5,10,44). However, realizing this potential at scale is constrained by major logistical and economic challenges, particularly inadequate and poorly harmonized post-harvest processing infrastructure and the susceptibility of fresh jackfruit to fungal pathogens, which can reduce both fresh-fruit marketability and the quality of feedstock available for post-harvest processing (1,2,66).

## 4. Zero-Waste Volariaztion of Jackfruit By-Products: Towards a Circular Bioeconomy

### 4.1 Scale and composition of the jackfruit waste stream

The jackfruit waste stream is substantial, comprising fruit peel, seeds, rag, non-edible core tissues, and, in some production systems, leaves. During processing, approximately 50–70% of the fruit weight may be discarded as waste, representing a considerably higher waste fraction than that of many other commercial fruits (2,66). Without appropriate management or valorisation, this large volume of residual biomass generates disposal costs and contributes to environmental pollution at both individual processing-unit and regional scales, particularly in major jackfruit-producing countries (2). Despite being commonly treated as waste, these residues contain substantial amounts of cellulose, hemicellulose, pectin, resistant starch, protein, and phenolic compounds. Their diverse biochemical composition therefore makes jackfruit processing residues a significant but currently underutilized feedstock for biorefinery and value-added product development (1,2,65,66).

### 4.2 Bioenergy and Biochemical Products

The cellulosic and hemicellulosic fractions of jackfruit waste can be valorised through several pathways to produce renewable energy carriers and other value-added products. Biological conversion processes, including microbial fermentation of jackfruit peel and seed residues, have been explored for the production of bioethanol, biohydrogen, and biogas, providing potentially environmentally sustainable alternatives to fossil-fuel-derived energy (1,2). As a complementary thermochemical pathway, pyrolysis can convert jackfruit biomass into

biochar and bio-oil, with potential applications in soil amendment, carbon management, and adsorption of environmental contaminants (1,44). Jackfruit peel-derived materials have also been investigated as adsorbents for the removal of dyes, heavy metals, and other pollutants, demonstrating the potential of jackfruit residues to contribute to environmental remediation as well as industrial waste valorisation (2).

**4.3 Biochemicals, Pectin and Phenolic Extraction**

Jackfruit rag contains appreciable quantities of pectin, a commercially important polysaccharide widely used as a gelling agent, stabilizer, and functional food ingredient. Ultrasound-assisted acid extraction has been investigated as an efficient approach for recovering pectin from jackfruit rag, with response-surface methodologies such as central composite design being used to optimize extraction conditions and recovery yields (1). Beyond pectin, jackfruit processing residues are rich sources of phenolic antioxidants and other potentially valuable compounds, including flavour and aroma precursors such as ferulic acid and vanillin-related compounds. Microbial bioconversion of these residues can also generate valuable enzymes, including pectinases and bromelain-like proteases, further supporting the potential of jackfruit waste as a biorefinery feedstock (1,2).

**4.4 Biodegradable and Active Food Packaging**

The conversion of jackfruit peel and seed residues into sustainable packaging materials represents an emerging strategy for simultaneously addressing food waste and dependence on petroleum-derived plastics. Nanocellulose recovered from jackfruit peel through acid hydrolysis can be combined with plasticizers such as glycerol or polyvinyl alcohol and natural fillers, including Boswellia serrata resin, to produce films with promising mechanical and barrier properties for potential packaging applications (69,70). Similarly, cellulose isolated from jackfruit peel has been blended with polyvinyl alcohol to produce biodegradable composite films, with Fourier-transform infrared spectroscopy (FTIR) and X-ray diffraction analyses supporting successful polymer interactions and film formation (69).

Jackfruit seed starch has also been incorporated into polyvinyl alcohol-based films containing natural pH-sensitive anthocyanin indicators derived from purple sweet potato peel. These “intelligent” packaging films can indicate changes in product freshness through visible colour changes and have been investigated for monitoring perishable foods such as shrimp (72). In another approach, pectin extracted from the mucilaginous sheath tissue of jackfruit has been ionically crosslinked to produce functional films with potential applications in active and intelligent food packaging (72). Jackfruit-derived extracts have additionally been incorporated into edible synbiotic films containing soy protein isolate, nanocellulose, and probiotic Lactobacillus strains for functional coating of dairy products such as feta cheese. These coatings have demonstrated antimicrobial activity against common foodborne pathogens, including Escherichia coli, Salmonella typhi, Shigella flexneri, and Staphylococcus aureus (44).

**4.5 Postharvest Packaging for Fresh Jackfruit**

In addition to by-product valorisation, considerable research has focused on extending the shelf life of whole and fresh-cut jackfruit through modified-atmosphere packaging, edible coatings, antimicrobial active packaging, and, more recently, nanotechnology- and intelligent-packaging-based approaches (71). However, this research area remains relatively limited compared with the extensive postharvest technology available for major commodity fruits. These packaging technologies should be viewed as complementary to, rather than substitutes for, disease-resistance strategies discussed elsewhere in this review. Postharvest packaging can reduce physiological deterioration and secondary microbial spoilage after harvest, but it cannot prevent the primary pathogen infections that originate in the field.

**4.6 A circular approach towards a Zero Waste model**

The valorisation pathways summarized above and in Table 2 demonstrate that most major jackfruit processing residues including seeds, peel, rag, latex, and core tissues could potentially be diverted from waste streams into value-added applications spanning food ingredients, nutraceuticals, bioenergy, biomaterials, and environmental remediation (1,2,44,65,66). Realizing a commercially viable zero-waste jackfruit model, however, will require integrated processing infrastructure capable of efficiently separating different waste fractions and directing them towards appropriate downstream applications. Continued optimization of extraction and conversion technologies will also be necessary to improve product yield, purity, process efficiency, and cost competitiveness relative to conventional feedstocks (1,65).

Importantly, the economic viability of such a circular bioeconomy is ultimately linked to the availability of a stable and increasing supply of raw jackfruit. Sustaining and expanding this supply will require addressing major biological constraints to production, particularly fungal diseases. Thus, disease resistance is not only important for improving fruit yield and quality but is also a prerequisite for realizing the full value-addition and circular-bioeconomy potential of the jackfruit production system.

## 5. Production Limiting Factors for Jackfruit – Fungal and Other Biotic Threats

**5.1 The Global Burden of Fungal Plant Pathogens**

Fungal and fungal-like pathogens, particularly oomycetes, represent among the most important biotic constraints on global crop production. Across major food crops, these pathogens are estimated to account for losses of up to 20% before harvest and a further 10% after harvest (13-16). Historical epidemics, including the Irish potato famine, coffee leaf rust in Ceylon, and southern corn leaf blight in the United States, illustrate the capacity of fungal diseases to cause catastrophic agricultural and economic losses (13,16). Modern agricultural

intensification, particularly large-scale monoculture using genetically uniform planting material, can further increase crop vulnerability. At the same time, the emergence of more virulent and fungicide-resistant pathogen populations, together with climate change, is increasing the risk by expanding the geographic distribution and seasonal activity of many fungal pathogens (13,14,16,17).

These challenges are particularly important for perennial tree crops. Their long generation times slow the development and deployment of new resistant varieties through conventional breeding, making it difficult for breeding programmes to respond rapidly to evolving pathogen populations. Jackfruit is subject to several fungal diseases that are also important in other tropical and subtropical orchard crops, further highlighting the need for disease-management strategies that can provide durable host resistance (63,64).

**5.2 Rhizopus Fruit Rot is the major fungal disease of jackfruit**

Rhizopus soft rot, caused predominantly by Rhizopus stolonifer and historically referred to by several synonyms, including Mucor stolonifer, Rhizopus artocarpi, and Rhizopus oryzae, is among the most economically important fungal diseases affecting jackfruit (11,12). Unlike Rhizopus infections in many other fruits and vegetables, where infection generally requires a wound, Rhizopus rot of jackfruit can affect flowers and fruits at multiple developmental stages, either directly or through wounds associated with sap-sucking insect activity (11,12).

Initial symptoms appear as soft, brown, water-soaked lesions on flowers and young fruits. These lesions rapidly develop white mycelial growth and black sporangia, producing the characteristic fuzzy or powdery appearance of infected tissues. Under severe disease pressure, fruits may become shrunken, blackened, and mummified (11,12). Warm, humid, and rainy conditions favour disease development, while airborne spores can facilitate secondary spread through wind, rain, and vectors (11,12). In affected jackfruit orchards in India, Rhizopus infection has been associated with estimated losses of approximately 15-32%. Importantly, no jackfruit cultivar has yet been identified with strong, naturally occurring resistance to this pathogen (11,12).

Management of Rhizopus rot is currently based primarily on cultural and chemical measures. Recommended practices include pruning to improve canopy ventilation and reduce humidity, removal and destruction of infected flowers and fruits, prevention of waterlogging around the root zone, and careful harvesting and handling to minimize mechanical injury. Under high disease pressure, copper-based or other registered fungicides may also be applied (11,12). Biological control has shown promise, with rhizosphere associated bacteria such as Burkholderia cenocepacia and lactic acid bacteria such as Lactococcus lactis subsp. lactis demonstrating inhibition of R. stolonifer in vitro and reductions in disease incidence in whole plants or post-harvest fruit (12). Such approaches may offer more sustainable alternatives to synthetic fungicides, particularly where reduced pathogen sensitivity to fungicides has been reported (12).

Nevertheless, these interventions primarily reduce pathogen populations or disease expression and do not establish stable, genetically encoded resistance in the host plant. This limitation strengthens the rationale for investigating genome-editing approaches capable of modifying host susceptibility or defence pathways, as discussed in Section 7.

**5.3 Anthracnose (Colletotrichum spp.)**

Anthracnose is an important pre- and post-harvest disease of tropical and subtropical fruit crops, including jackfruit, mango, papaya, banana, citrus, and avocado (73–75). It is caused by several Colletotrichum species, particularly C. gloeosporioides and closely related taxa within the C. gloeosporioides species complex. The pathogen commonly establishes a latent biotrophic infection in immature fruit without producing visible symptoms and subsequently switches to a necrotrophic phase as the fruit ripens (68,73,75). During this stage, characteristic sunken, dark-brown to black lesions develop and may expand and coalesce across much of the fruit surface (68,73,75).

The latent nature of anthracnose makes the disease particularly difficult to manage. Fruit may appear healthy at harvest but subsequently develop severe symptoms during storage, transport, and marketing, resulting in substantial economic losses and reduced marketability (73,75). Increasing regulatory and consumer concerns regarding fungicide residues in food and the widespread capacity of fungal pathogens to develop fungicide resistance have stimulated research into more sustainable disease-management approaches. These include biological control using antagonistic yeasts and bacteria, natural antimicrobial coatings based on compounds such as chitosan and essential oils, and emerging nanotechnology- and genome-editing-based strategies (68,73–75).

**5.4 Dieback, Leaf Spot and Other Fungal Diseases**

In addition to Rhizopus rot and anthracnose, jackfruit is affected by several other fungal diseases of agronomic importance (Table 2). Dieback associated with Lasiodiplodia theobromae can cause progressive browning, wilting, and death of branches, potentially reducing tree productivity and longevity. Leaf spot caused by Phyllosticta artocarpina and pink disease caused by Botryobasidium salmonicola are generally considered less economically important but can nevertheless affect tree health and productivity. These diseases can be managed to some extent through orchard sanitation and targeted fungicide applications; however, as with the major fungal diseases, well-characterized jackfruit cultivars with strong genetic resistance have not been identified (16).

**5.5 Implications for jackfruit as a Food Security Crop**

The cumulative effects of fungal diseases represent a major constraint to the development of jackfruit as a climate-resilient food-security crop. Under severe disease pressure, losses in marketable fruit production can

approach one-third of the crop, while infections can also compromise fruit quality for both fresh consumption and processing (11,12). Continued dependence on fungicide applications adds further environmental, economic, and food-safety considerations (13,14,73). These constraints are particularly significant because the economic value of jackfruit extends beyond fresh fruit sales to the processing and valorisation of seeds, peel, rag, and other by-products. Disease-related reductions in fruit yield and quality therefore have implications throughout the emerging jackfruit value chain.

Table 2 summarizes the principal fungal pathogens reported in jackfruit, their causal agents, characteristic symptoms, current management approaches, and the limited evidence for genetic resistance. The widespread absence of well-characterized resistant cultivars across the major disease categories provides a strong rationale for exploring genome-editing strategies as a complementary approach to conventional disease management.

## 6. Limitations of Conventional Approaches to Disease Resistance Breeding in Jackfruit

Conventional breeding for disease resistance generally involves identifying resistance sources containing suitable resistance genes in cultivated germplasm, wild relatives, or related species and subsequently introgressing these traits into elite cultivars through repeated crossing and selection (58,59). Several biological and genetic characteristics of jackfruit make this approach particularly challenging. Jackfruit is a long-lived perennial tree with a long juvenile period. Trees may require approximately 10 years or more to reach maturity and begin substantial fruit production, in contrast to annual crops, which can complete several breeding generations within a relatively short period (3,63,64). Consequently, conventional breeding cycles in jackfruit are inherently slow and require substantial land, labour, and time for field evaluation. There is currently no well-established jackfruit cultivar or wild relative known to possess strong natural resistance to the two major diseases, Rhizopus rot and anthracnose. The absence of a clearly defined resistant donor genotype therefore represents a fundamental obstacle to conventional resistance breeding because there may be no readily available resistance trait to introgress. Jackfruit exhibits substantial genetic heterozygosity. Genomic analysis of the Bangladeshi cultivar BARI Kanthal-3 reported a heterozygosity rate of approximately 1.62%, with around 90% of identified single-nucleotide polymorphisms (SNPs) located in intergenic regions (64). Such genetic complexity can complicate the development and selection of segregating populations and the identification of favourable allele combinations through conventional breeding.

Jackfruit is propagated both sexually through seed and clonally through vegetative methods. Elite high-yielding clones often possess combinations of fruit-quality, yield, and agronomic traits that growers seek to preserve. Conventional crossing can disrupt these favourable genetic combinations, potentially resulting in progeny that no longer retain the characteristic attributes of the elite clone (63,64). Similar limitations have been encountered in other clonally propagated perennial crops, including banana and citrus, where long generation times, sterility, polyploidy, or other reproductive constraints can substantially slow conventional breeding programmes (30–33). These limitations collectively define a setting in which genome editing may offer particular advantages.

CRISPR–Cas9 and related genome-editing technologies can introduce targeted genetic modifications directly into elite, locally adapted cultivars without requiring repeated crossing or the identification of a naturally resistant donor. This is especially advantageous where the breeding objectives involve long-generation crops, high heterozygosity, limited resistance germplasm, or preservation of elite clonal backgrounds (37, 38, 58, 59). Furthermore, genome-editing strategies that ultimately produce plants without stable transgene sequences could potentially enable targeted disease-resistance modifications while avoiding the introduction of foreign DNA into the final edited genome. These characteristics make CRISPR–Cas an especially promising complementary strategy for developing disease-resistant jackfruit cultivars.

## 7. CRISPR-Cas Genome Editing: Principles and Molecular Toolbox

### 7.1 Origins and Basic Mechanism

CRISPR and its associated Cas proteins constitute an adaptive immune system found in many bacteria and archaea, where they recognize and eliminate invading genetic material from plasmids and bacteriophages (26,37,59). The CRISPR–Cas9 system has subsequently been adapted as a versatile genome-editing platform. It uses a synthetic single-guide RNA (sgRNA) to direct the Cas9 endonuclease to a complementary genomic sequence adjacent to a short protospacer-adjacent motif (PAM) (45,59). Upon target recognition, Cas9 introduces a DNA double-strand break (DSB) at the target locus (45,59). The resulting DSB can be repaired through two principal endogenous pathways. Non-homologous end joining (NHEJ) is an error-prone mechanism that frequently generates small insertions or deletions (indels), which can disrupt gene function and thereby provide an efficient route to gene knockout (44,53). Homology-directed repair (HDR), in contrast, uses a homologous donor DNA template to introduce a defined sequence modification at the target locus (53). The ability of CRISPR-Cas9 to function both as an efficient gene-knockout tool and, under appropriate conditions, as a platform for precise sequence modification has made it valuable for fundamental plant biology and crop improvement (37,45,53).

### 7.2 Expanded CRISPR Toolbox: Cas12a, Base Editing and Prime Editing

The CRISPR toolbox has expanded substantially beyond Cas9 to include alternative nucleases and editing platforms. Cas12a, formerly known as Cpf1, is a class 2 CRISPR effector that recognizes a different, typically T-rich PAM and generates staggered rather than blunt DNA ends. In some applications, Cas12a has produced larger deletions and improved editing outcomes, including enhanced HDR efficiency, thereby expanding the

range of genomic targets accessible to CRISPR editing (32). Base editing provides a further refinement by enabling targeted nucleotide conversion without creating a conventional DNA double-strand break. Base editors generally combine a catalytically impaired or nickase Cas protein with a deaminase enzyme capable of directly converting one base pair into another. Cytosine base editors can convert C•G to T•A, whereas adenine base editors can convert A•T to G•C at defined target sites (39,40,45). Prime editing represents a further development of this technology. It combines a Cas9 nickase with an engineered reverse transcriptase and an extended prime-editing guide RNA (pegRNA), which specifies the target site and carries a template encoding the desired sequence change (41–44). Prime editing can, in principle, generate all 12 possible base-to-base substitutions as well as small, precisely defined insertions and deletions without requiring a conventional DSB or an exogenous donor DNA template. It therefore offers considerable flexibility for correcting or introducing small-scale genetic variants while potentially reducing the bystander modifications associated with some base-editing approaches. However, prime-editing efficiencies in planta remain generally lower than those achieved with conventional Cas9-mediated knockout, and optimization of the technology remains an active area of research (42,43,50). In addition to loss-of-function approaches targeting susceptibility (S) genes, CRISPR technology can be used for gain-of-function strategies that activate endogenous defence pathways. Catalytically inactive Cas9 (dCas9), when fused to transcriptional activator domains, can be targeted to regulatory regions to enhance the expression of otherwise weakly expressed or silenced plant defence genes (52).

### 7.3 Delivery systems: From Transgenic constructs to DNA-Free Editing

The development of effective delivery systems is essential for translating CRISPR technologies into practical plant genome editing. The two most widely established approaches are Agrobacterium-mediated T-DNA transformation and particle bombardment (biolistics), both of which can introduce CRISPR components through plasmid-based constructs. Although these approaches are effective across many plant species, stable integration and prolonged expression of foreign DNA raise both regulatory and scientific concerns. These include the potential classification of edited plants as genetically modified organisms (GMOs) in some jurisdictions, prolonged Cas expression that may increase the opportunity for off-target editing, and variation in editing efficiency associated with the genomic site of transgene integration (61,73.

To address these limitations, DNA-free approaches have been developed in which Cas9 or Cas12a is delivered as a preassembled ribonucleoprotein (RNP) complex with a synthetic guide RNA. RNPs can be introduced into plant protoplasts, for example through polyethylene glycol (PEG)-mediated transfection, or delivered into plant tissues using particle bombardment (53–57,71,74–79). Because the editing machinery is transiently present and does not require stable integration of a CRISPR construct, RNP-based editing can reduce the duration of Cas nuclease activity and eliminate constitutive transgene expression.

Transgene-free RNP-mediated editing and subsequent regeneration have been demonstrated in several crops, including wheat, rice, lettuce, potato, tobacco, grapevine, apple, maize, and citrus (54–57,61,71,74). This approach is particularly attractive for orphan and perennial fruit crops such as jackfruit, where public acceptance, regulatory classification, and preservation of elite clonal backgrounds may represent important barriers to the adoption of conventional transgenic technologies.

## 8. CRISPR-Cas-Mediated Engineering of Fungal Disease Resistance: Validated Case Studies in Related Crops

### 8.1 The Susceptibility (S)-Gene Editing Strategy

One of the most promising approaches for engineering durable disease resistance using CRISPR–Cas is the identification and disruption of host susceptibility (S) genes. These genes do not directly encode resistance but are exploited by pathogens to establish or maintain compatible infections. Loss-of-function mutations in such genes can therefore produce a form of recessive resistance (20–22,38,50).

S-gene editing is particularly attractive for long-generation, highly heterozygous, clonally propagated crops such as jackfruit. Conventional breeding would require the identification and introgression of a suitable resistance allele, often through multiple generations of crossing and selection. CRISPR editing, in contrast, can potentially introduce a targeted loss-of-function mutation directly into an elite cultivar without disrupting the broader genetic background responsible for desirable agronomic and fruit-quality traits (38,50).

### 8.2 MLO-Mediated Powdery Mildew Resistance: A Paradigm Case

One of the best validated examples of S-gene editing for fungal disease resistance involves the MLO (Mildew Locus O) gene family. A landmark study demonstrated that simultaneous CRISPR–Cas9 knockout of all three homoeologous copies of TaMLO in hexaploid bread wheat produced heritable resistance to powdery mildew caused by Blumeria graminis f. sp. tritici, without a detectable growth penalty (19,27). This study provided an important demonstration that multiple homologous gene copies can be simultaneously targeted in a complex polyploid crop genome.

Subsequent disruption of the corresponding TaEDR1 gene family further demonstrated that progressively increasing the number of disrupted gene copies could enhance powdery mildew resistance, with triple mutants showing strong resistance phenotypes (20). In tomato, introduction of a 48-bp deletion in SlMLO1 through CRISPR editing produced transgene-free plants resistant to powdery mildew caused by Oidium neolycopersici, without significant effects on plant growth or fruit production in the reported generations (18,27).

MLO editing has also been investigated in grapevine, where targeting VvMLO7 in protoplasts enhanced fungal resistance at the cellular level, although whole-plant regeneration from these edited protoplasts has not yet been reported (27). The repeated identification of MLO-mediated susceptibility mechanisms across taxonomically diverse hosts—including wheat, tomato, and grapevine—suggests that MLO orthologues represent a broadly conserved and potentially tractable class of fungal-disease susceptibility targets. This provides a strong rationale for investigating corresponding MLO genes in jackfruit, particularly given the importance of fungal diseases across tropical and subtropical tree crops (19–21,27).

**8.3 Citrus Canker: LOB1 Susceptibility-Gene and Base-Editing Strategies**

Citrus canker provides another influential example of susceptibility-gene editing in a perennial fruit crop. Although citrus canker is a bacterial rather than fungal disease, it provides an important technical model for disease-resistance engineering in tree fruits. The disease is caused by Xanthomonas citri subsp. citri (Xcc), which exploits the host susceptibility gene CsLOB1.

Modification of the effector-binding element within the CsLOB1 promoter in Duncan grapefruit and Wanjincheng sweet orange increased resistance to Xcc, with resistance generally associated with the extent of disruption within the promoter region (22,23,36). Subsequent application of Cas12a to the CsLOB1 promoter and the CsPDS marker locus further demonstrated the utility of this nuclease for generating targeted deletions in citrus (32,36).

More recently, adenine base editing has been used to modify the LOB1 promoter without introducing a conventional DSB, generating transgene-free citrus lines with enhanced canker resistance and, in some lines, altered polyphenolic profiles (24,36). Additional editing of CsWRKY22, a transcription factor induced during Xcc infection and apparently functioning as a negative regulator of canker resistance, has provided another example of how manipulation of distinct susceptibility or immune-regulatory loci can improve disease resistance (32).

Together, these studies illustrate the progressive development of CRISPR-based disease-resistance strategies in a clonally propagated perennial fruit crop: from Cas9-mediated knockout, through promoter editing and base editing, to the application of alternative nucleases such as Cas12a. The biological similarities between citrus and jackfruit—including long juvenile periods, high heterozygosity, and vegetative propagation of elite genotypes—make these studies particularly relevant as technical precedents for jackfruit improvement.

**8.4 Banana – A Directly Analogous Tropical Tree Fruit Crop**

Banana (Musa spp.) provides one of the most directly relevant precedents for jackfruit because it is a clonally propagated tropical fruit crop with a complex genome, long production cycle, substantial biotic-stress pressure, and limited sources of resistance within cultivated germplasm (30,31,33,34). As a proof of principle, CRISPR–Cas9 has been successfully used to disrupt the phytoene desaturase (PDS) gene in banana. In the commercially dominant Cavendish background, very high mutation frequencies were reported among regenerated plants, demonstrating the feasibility of efficient CRISPR editing in this genetically challenging crop (33,34).

Further work has explored CRISPR-based manipulation of disease-related genes in banana, including suppression of the susceptibility gene MusaDMR6 and modification of defence-associated genes such as chitinase, with the broader objective of improving resistance to major biotic constraints, including bacterial wilt and viral diseases (31). CRISPR editing has also been used to modify the banana 1-aminocyclopropane-1-carboxylic acid oxidase (MaACO1) gene, substantially extending natural post-harvest fruit shelf life from approximately 21 to 80 days (29,32). This is particularly relevant to jackfruit because rapid ripening and subsequent susceptibility to secondary fungal spoilage are important post-harvest constraints.

The demonstrated feasibility of gene knockout, S-gene modification, defence-gene manipulation, and ripening-pathway editing in a clonally propagated tropical fruit crop provides strong technical encouragement for analogous applications in jackfruit. However, successful translation will depend on identifying appropriate jackfruit targets and establishing efficient tissue-culture, transformation, or protoplast-regeneration systems (30–34).

**8.5 Cassava and Cacao: Other Examples of Tropical Perennial Crops**

CRISPR technology has also been applied to other clonally propagated tropical staple and tree crops. In cassava (Manihot esculenta), knockout of the eIF4E isoforms nCBP-1 and nCBP-2, which are exploited by cassava brown streak virus, increased resistance to this economically important viral disease (25,63). Although this example concerns a virus rather than a fungal pathogen, it illustrates the broader potential of targeting host factors required for pathogen infection.

A more directly relevant example comes from cacao (Theobroma cacao), where CRISPR–Cas9-mediated disruption of TcNPR3, a negative regulator of plant immune signalling, enhanced defence responses and resistance to the fungal-like oomycete pathogen Phytophthora tropicalis (26,27). This demonstrates that resistance can also be enhanced by removing negative regulators of innate immune signalling rather than simply disrupting pathogen susceptibility factors. Because many components of plant immune signalling are conserved across angiosperms, analogous strategies could potentially be investigated in jackfruit.

**8.6: Collecting evidence for the Case Study**

Table 3 summarizes validated CRISPR–Cas gene-editing studies in wheat, tomato, grapevine, citrus, banana, cassava, and cacao, including the target gene or locus, editing technology, and resulting disease-resistance phenotype (35). Collectively, these studies reveal several recurring principles: the conservation of susceptibility-

gene families and immune regulators across diverse crops; the feasibility of CRISPR editing in clonally propagated, heterozygous, and long-generation crops; and the progressive expansion of editing precision from conventional Cas9-mediated knockout to Cas12a, base editing, and prime editing.

These findings provide both a conceptual and technical framework for exploring disease resistance in jackfruit. They are also consistent with broader reviews documenting the expanding application of CRISPR-based approaches to pathogen resistance across staple and horticultural crops (46–49,51).

## 9. Prospects and Proposed Roadmap of CRISPR-mediated Fungal Disease resistance in Jackfruit

### 9.1 Genomic Resources now available

A prerequisite for applying CRISPR to jackfruit improvement is a sufficiently resolved reference genome from which candidate susceptibility genes can be identified and guide RNAs designed. A major advance was the publication of a draft whole-genome sequence of jackfruit in 2019–2020. The assembly comprised approximately 982 Mb and contained 35,858 predicted genes, alongside a genome assembly for the closely related breadfruit species Artocarpus altilis (63). The analysis identified expansions in gene families associated with starch and sucrose metabolism, consistent with the characteristic carbohydrate-rich composition of jackfruit, while also providing a genomic foundation for trait mapping and candidate-gene discovery.

A complementary high-quality genome sequence has subsequently been generated for the high-yielding, extended-fruiting Bangladeshi cultivar BARI Kanthal-3. This resource provides additional information on within-species genetic variation, including an estimated heterozygosity of approximately 1.62%, and provides comparative genomic information relevant to the extended fruiting-season phenotype (64).

Together, these genomic resources make it technically feasible to begin a targeted genomic strategy for disease-resistance improvement in jackfruit. In particular, they provide the foundation for identifying jackfruit orthologues of validated susceptibility and defence-related genes, including MLO- and NPR3-type candidates, and for designing candidate guide RNAs for subsequent functional validation.

### 9.2 Proposed Target-gene Identification and Editing Strategy

Based on the genomic resources and comparative evidence reviewed above, we propose an incremental strategy for developing CRISPR-mediated fungal disease resistance in jackfruit.

The first stage should involve comparative genomic identification of jackfruit orthologues of validated susceptibility genes. MLO family genes represent an important candidate class because their role in fungal susceptibility has been demonstrated across wheat, tomato, and grapevine (19–21,27). Similarly, jackfruit orthologues of NPR3-type negative immune regulators, whose disruption has enhanced resistance to Phytophthora tropicalis in cacao, represent potential candidates for improving resistance to major jackfruit pathogens (26).

The second stage should involve functional validation of candidate genes using transient CRISPR–Cas9 or RNP-based editing in jackfruit protoplasts or callus cultures. Experimental approaches developed in citrus, grapevine, and banana could provide useful technical precedents for delivery and recovery of edited cells (54–56,71).

The third stage should focus on regeneration of edited plantlets, preferably using DNA-free RNP delivery where technically feasible. Following regeneration, edited plants should undergo molecular characterization, controlled pathogen-inoculation assays, and evaluation of agronomic performance and fruit quality. Promising lines would subsequently require multi-season and multi-location field evaluation to determine whether resistance is durable under natural disease pressure.

### 9.3 Technical Challenges Specific to Jackfruit

Several technical barriers must be addressed before this roadmap can be implemented. The most immediate is the lack of a standardized, highly efficient system for jackfruit tissue culture, protoplast isolation, and plant regeneration. Such systems are considerably more developed in crops such as citrus and banana, whereas jackfruit-specific regeneration technology remains comparatively limited (54,55,71). Establishing a reliable protoplast isolation and regeneration protocol, or alternatively an efficient Agrobacterium-mediated transformation system, is therefore a critical prerequisite for practical genome editing in jackfruit (54–56,71).

A second challenge concerns off-target editing. Guide-RNA specificity has not yet been comprehensively characterized in jackfruit, making rigorous computational guide design and experimental validation essential. Available mitigation strategies include the use of high-fidelity Cas9 variants, in silico prediction and selection of highly specific guide RNAs, and transient RNP delivery to restrict the duration of nuclease activity within cells (28,39,53,58,62).

Third, candidate-gene identification should be supported by transcriptomic and functional-genomic analyses of the jackfruit–Rhizopus and jackfruit–Colletotrichum interactions. Cross-species orthology provides valuable candidate genes, but it cannot substitute for direct evidence of the molecular mechanisms underlying susceptibility in jackfruit. This is particularly important for diseases caused by necrotrophic pathogens, for which susceptibility mechanisms may differ substantially from those characterized in better-studied pathosystems (11,12,63,64).

### 9.4 Complementary and Synergistic Strategies

CRISPR-based genetic improvement should be viewed as one component of an integrated jackfruit improvement strategy rather than as a replacement for existing disease-management and value-addition technologies. During the relatively long period required to develop, evaluate, and deploy genome-edited

cultivars, improved post-harvest packaging, biological control, orchard sanitation, and other disease-management measures can reduce losses and stabilize supply chains (1,2,12,44,66,71).

Likewise, the zero-waste valorisation strategies described in Sections 3 and 4 can increase the economic value recovered from harvested fruit by converting seeds, peel, rag, and other residues into food ingredients, nutraceuticals, biomaterials, bioenergy, and other products. An integrated approach combining genetic resistance, improved disease management, post-harvest technologies, and waste valorisation therefore offers the strongest pathway towards establishing jackfruit as a commercially viable, climate-resilient food crop (Figure 1).

## 10. Regulatory, Ethical, and Public Acceptance Considerations

The regulatory status of genome-edited crops varies substantially among jurisdictions and will strongly influence the pathway by which genome-edited jackfruit cultivars could reach farmers and consumers. In several countries, certain genome edits that do not involve the introduction of exogenous DNA—particularly small insertions or deletions generated through site-directed nuclease type 1 (SDN1) approaches—may be treated differently from conventional transgenic GMOs. Similarly, some precisely targeted sequence changes generated through template-dependent approaches may receive regulatory treatment distinct from that applied to transgenic crops, depending on the jurisdiction (58,59).

By contrast, SDN3 approaches involving the insertion of larger DNA sequences or complete genes through homologous recombination are more likely to fall under regulatory frameworks comparable to those governing conventional genetically modified organisms because they introduce exogenous genetic material (59). Since many S-gene knockout strategies rely on simple indel formation, DNA-free RNP-mediated editing could potentially offer a comparatively favourable regulatory pathway in jurisdictions that distinguish such edits from transgenic modification (56,58,59).

Regulatory convergence, however, remains incomplete. The European Union has historically applied a comparatively stringent regulatory framework to genome-edited organisms, although policy reforms and proposals concerning the regulation of certain new genomic techniques have continued to evolve (58,59). Differences among national regulatory systems have important implications for international trade in genome-edited planting material and processed food products. Transparent communication, appropriate labelling where required, public engagement, and continued international dialogue will therefore be important as genome-edited fruit crops progress towards commercialization.

Ethical and socioeconomic considerations are equally important. Jackfruit is predominantly produced by smallholder and homestead farmers in low- and middle-income regions, making equitable access to genome-editing technologies a central consideration. Intellectual-property rights associated with CRISPR reagents, transformation systems, and proprietary gene-editing technologies may affect accessibility and technology transfer. Maintaining genetic diversity within jackfruit germplasm should also remain a priority so that disease resistance is not accompanied by excessive genetic uniformity. These issues should be incorporated into research and policy planning from the earliest stages of genome-editing programmes (58–60).

## 11. Future Research Priorities

The evidence reviewed here identifies several immediate research priorities for advancing genome-edited disease resistance in jackfruit. First, highly optimized tissue-culture, protoplast-isolation, transformation, and plant-regeneration systems need to be established. This is currently one of the most important technical bottlenecks for initiating a practical CRISPR-based improvement programme in jackfruit (54,55,71).

Second, comparative and functional genomic studies should characterize the molecular basis of jackfruit susceptibility to Rhizopus and Colletotrichum. The existing genome resources provide a foundation for this work (63,64), but species-specific functional validation is required to progress beyond inference based solely on orthology and to identify robust targets for disease-resistance engineering.

Third, continued development and optimization of DNA-free CRISPR delivery systems specifically adapted to jackfruit tissues will be important for improving editing efficiency while potentially simplifying downstream regulatory considerations (53,54,56–58). Fourth, integrated techno-economic analyses across the entire jackfruit value chain are needed to quantify the potential economic benefits of combining disease-resistant germplasm with the valorisation of processing by-products. Such analyses could help public-sector research institutions, farmers, and industry prioritize investments in breeding, processing, and infrastructure (1,2,65,66).

Finally, realizing the full potential of genome editing in jackfruit will require long-term interdisciplinary collaboration among plant pathologists, molecular geneticists, genome-editing specialists, food technologists, breeders, economists, and regulatory scientists. Such collaboration will be essential to ensure that improved jackfruit cultivars are not only technically effective but also economically accessible and suitable for the farmers who depend on the crop.

## 12. Conclusion

Jackfruit occupies a distinctive position among the world's underutilized fruit crops, combining a rich nutritional and phytochemical profile with expanding opportunities in functional foods, plant-based proteins, and the circular valorisation of its unusually large processing by-product stream. Seeds, peel, rag, core tissues, and other residues offer opportunities for conversion into food ingredients, nutraceuticals, bioenergy, biomaterials, and biodegradable packaging materials. However, the full realization of this potential remains constrained by

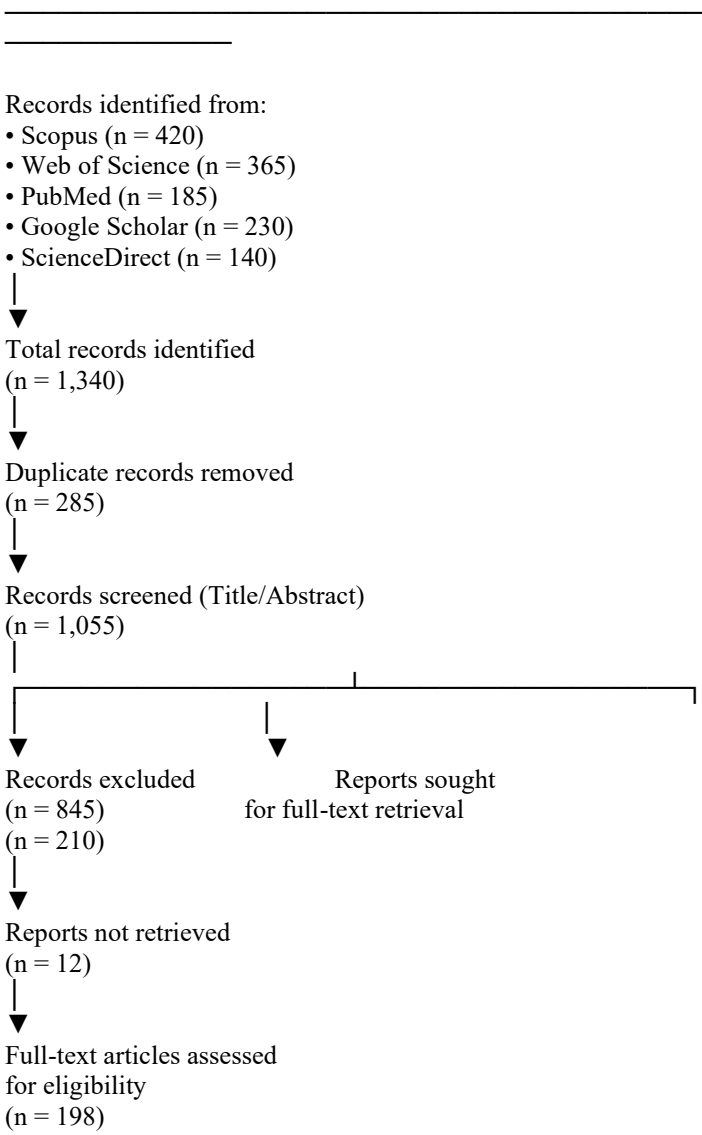
persistent fungal diseases, particularly Rhizopus fruit rot and anthracnose, for which strong natural resistance has not yet been identified in cultivated jackfruit.

Conventional breeding faces substantial obstacles because of the crop's long generation time, high heterozygosity, limited resistance germplasm, and widespread reliance on vegetative propagation of elite clones. The rapid development of CRISPR–Cas genome-editing technologies provides a potentially transformative complementary strategy. Validated applications in wheat, tomato, grapevine, citrus, banana, cassava, and cacao demonstrate that susceptibility-gene knockout, immune-regulator modification, base editing, and other genome-editing approaches can be used to enhance disease resistance in diverse crops, including clonally propagated perennial species.

The availability of jackfruit genome sequences now provides the foundation for identifying candidate susceptibility and defence-related genes and for developing a species-specific genome-editing strategy. Realizing this potential will nevertheless require substantial investment in jackfruit-specific tissue culture, transformation and regeneration systems, functional characterization of candidate genes, DNA-free delivery technologies, controlled disease-screening platforms, and field validation. The regulatory and socioeconomic dimensions of genome-edited crops must also be addressed carefully, particularly given the importance of jackfruit to smallholder production systems.

Taken together, the convergence of genomic resources, genome-editing technologies, disease-management strategies, and growing markets for jackfruit-derived products provides a credible pathway for transforming jackfruit from an underutilized crop into a more productive, disease-resilient, and economically valuable component of sustainable food systems. The integration of durable genetic resistance with zero-waste valorisation and improved post-harvest management could therefore strengthen both the climate resilience and food-security contribution of jackfruit in the twenty-first century.

**Figure 1: PRISMA FLOW DIAGRAM**



Full-text articles excluded (n = 118)
• Not related to jackfruit (n = 32)
• No zero-waste valorization data (n = 24)
• No CRISPR/genome editing information (n = 20)
• Conference abstracts/reviews only (n = 18)
• Insufficient experimental information (n = 15)
• Non-English articles (n = 9)

Studies included in qualitative review
(n = 80)

**Figure 2. Integrated Framework for Zero-Waste Jackfruit Valorization and CRISPR-Enabled Fungal Disease Resistance**

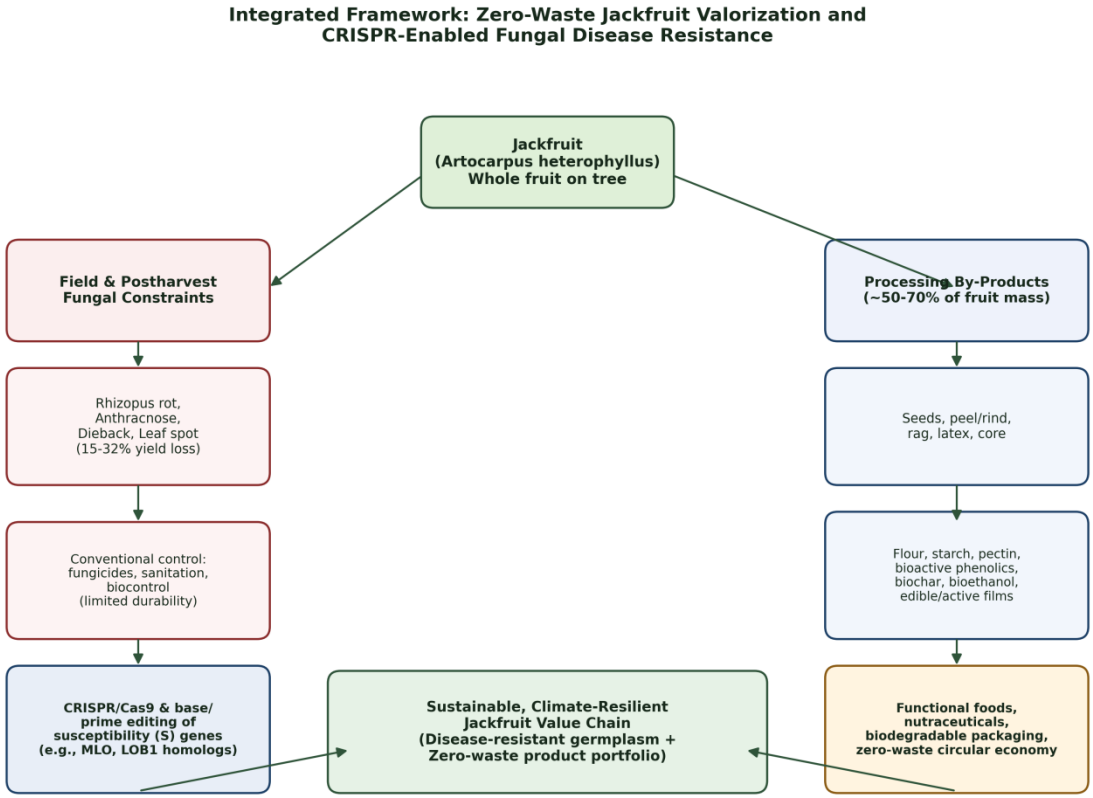



Figure legend: Original schematic prepared by the authors, linking the major fungal disease constraints affecting jackfruit production and their proposed resolution through CRISPR-Cas9 and base/prime editing of susceptibility genes (left) with the zero-waste valorization of jackfruit processing by-products into functional food, nutraceutical, packaging and bioenergy products (right), converging on a sustainable, climate-resilient jackfruit value chain.

**Table 1. Nutritional and phytochemical composition of major jackfruit fruit fractions relevant to functional food development**

| Fruit fraction | Approx. share of fruit mass | Key macronutrients | Key bioactive/phytochemical constituents | Reported functional properties | Key sources |
|---|---|---|---|---|---|
| Ripe pulp (bulb) | 25-40% | Low fat; dietary fibre; sugars | Vitamin C, A, thiamine, riboflavin, niacin, folate; flavonoids, tannins, phenolic acids; carotenoids | Antioxidant; source of dietary fibre and micronutrients | 3, 4 |
| Seeds | 10-15% | Starch (12.9-17.9 g/100g); protein (~18%); fibre (1.6-3.9 g/100g); resistant starch (19.9-25.6 g/100g) | Catechin, ferulic acid, epicatechin, rutin, gallic acid; Mg, K, P, Na, Ca, Cu, Mn, Fe, Zn | Antioxidant, antidiabetic, anticancer, hepatoprotective, antimicrobial, anti-inflammatory; functional flour/starch for bakery, dairy fortification, microencapsulation | 4, 5, 7, 8, 10, 67 |
| Rind/peel | 20-30% | Cellulose, hemicellulose, pectin | Phenolic antioxidants; pectin polysaccharide | Feedstock for pectin extraction, biodegradable packaging films, activated carbon | 1, 2, 69, 70 |
| Rag/perianth waste | 10-15% | Pectin-rich fibre | Phenolic compounds | Optimized ultrasound-assisted pectin extraction; functional gelling ingredient | 1 |
| Latex | Trace-variable | Polyisoprene-type exudate | Proteins, alkaloids (traditional medicine use) | Adhesive/cementing applications, traditional wound care; allergenic potential | 2 |

Source: compiled by the authors from references cited in Section 3.

**Table 2. Major fungal diseases constraining jackfruit production, their causal agents, symptoms, and current management approaches**

| **Disease** | **Causal fungal agent(s)** | **Affected part(s)** | **Key symptoms** | **Reported yield impact** | **Resistance status** |
|---|---|---|---|---|---|
| Rhizopus (soft) fruit rot | Rhizopus stolonifer (syn. R. artocarpi), R. oryzae | Flowers, young & mature fruit | Soft, watery brown spots; black powdery sporangial mass; shrunken/mummified fruit | 15-32% crop loss | No resistant cultivar identified |
| Anthracnose | Colletotrichum gloeosporioides and related spp. | Fruit (pre- & post-harvest), leaves | Latent biotrophic infection; dark brown/black sunken lesions on ripening | Major post-harvest loss | No resistant cultivar identified |
| Dieback | Lasiodiplodiatheobromae (syn. Botryodiplodiatheobromae) | Branches, stem | Discoloration/wilting of branches from tip downward | Reduced tree vigour/productivity | No resistant cultivar identified |
| Leaf spot | Phyllostictaartocarpina | Leaves | Discrete necrotic leaf lesions | Minor; localized defoliation | Not characterized |
| Pink disease | Botryobasidiumsalmonicola | Branches, twigs | Pink bark encrustation; twig dieback | Minor; localized | Not characterized |

Source: compiled by the authors from references cited in Section 5.

**Table 3. Selected validated CRISPR-Cas genome-editing case studies for fungal (and analogous biotic) disease resistance in crops relevant to jackfruit improvement strategy**

| **Crop** | **Target gene/locus** | **Editing tool** | **Pathogen/disease targeted** | **Resistance outcome** | **Reference(s)** |
|---|---|---|---|---|---|

| Crop | Target gene/locus | Editing tool | Pathogen/disease targeted | Resistance outcome | Reference(s) |
|---|---|---|---|---|---|
| Bread wheat | TaMLO (3 homoeologs) | CRISPR-Cas9 knockout | Powdery mildew (Blumeria graminis f. sp. tritici) | Heritable resistance, no growth penalty | 19 |
| Bread wheat | TaEDR1 (3 homoeologs) | CRISPR-Cas9 knockout | Powdery mildew | Resistance increased with homoeologs edited | 20 |
| Tomato | SlMLO1 | CRISPR-Cas9 (48-bp deletion) | Powdery mildew (Oidium neolycopersici) | Transgene-free, stable across T1-T2 | 18 |
| Grapevine | VvMLO7 | CRISPR-Cas9 RNP (protoplast) | Powdery mildew/oomycete | Improved resistance in protoplasts | 27, 55 |
| Citrus (grapefruit, orange) | CsLOB1 promoter | Cas9; Cas12a; base editing | Citrus canker (Xanthomonas citri) | Progressive resistance; transgene-free lines | 22, 23, 24, 32, 36 |
| Sweet orange | CsWRKY22 | CRISPR-Cas9 knockout | Citrus canker | Increased resistance to Xcc | 32 |
| Cassava | nCBP-1, nCBP-2 (eIF4E) | CRISPR-Cas9 knockout | Cassava brown streak virus | Elevated viral resistance | 25, 26 |
| Cacao | TcNPR3 | CRISPR-Cas9 knockout (transient) | Phytophthora tropicalis (oomycete) | Enhanced defence & resistance | 26, 27 |
| Banana (Rasthali, Cavendish) | PDS (proof-of-concept) | CRISPR-Cas9 knockout | N/A (technical validation) | Up to 100% mutation rate in triploid genome | 33, 34 |
| Banana | MusaDMR6; chitinase upregulation | CRISPR-Cas9; CRISPRa | Xanthomonas wilt; viral disease | Enhanced disease tolerance | 31 |

Source: compiled by the authors from references cited in Section 8.

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**Authors' contributions**

KC contributed to the collection of articles and prepared the initial draft of the manuscript; CK formulated the concept and edited the manuscript; JA, SG and AS revised and edited the final manuscript. All authors 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.

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