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Review

Biology, Diagnostics, Pathogenomics and Mitigation Strategies of Jackfruit-Bronzing Bacterium *Pantoea stewartii* subspecies *stewartii*: What Do We Know So Far about This Culprit?

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Abstract: Jackfruit-bronzing disease, caused by *Pantoea stewartii* subsp. *stewartii*, has recently become more common in the jackfruit crop. Jackfruit-bronzing disease was first discovered in the Philippines in 2014 and spread to Malaysia and Mexico in 2017. Outbreaks of the disease reduced the quality of fresh jackfruit, lowered the market value of local jackfruit, and caused yield losses to the production and financial setbacks to the processors. This disease is more aggressive toward jackfruits with a sweeter flavor and high Brix composition. Symptoms are observable when the fruit is cut open, indicated by the appearance of rusty specks and yellowish-orange to reddish discoloration of the infected pulps and rags. Extensive research is needed to better understand the pathogen's nature and pathogenicity, supporting future disease prevention and recognition of the pathogen-host interaction. This review explores the significance of the jackfruit-bronzing bacterium, its biology, diagnostics, and pathogenomics, emphasizing the pathogen's virulence and the management strategies to mitigate this disease. Understanding this destructive bacterium will guide growers and agricultural practitioners to develop the most efficient and sustainable jackfruit-bronzing control methods.

Keywords: biology; jackfruit-bronzing; pathogenomics; *Pantoea stewartii* subspecies *stewartii*; taxonomy

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1. Introduction

Jackfruit (*Artocarpus heterophyllus* Lam) falls into the class *Magnoliopsida*, order *Rosales*, and belongs to the family *Moraceae* [1,2]. It is a non-seasonal fruit and a close relative of *Cempedak* (*Artocarpus integer*) and breadfruit (*Artocarpus altilis*). It is the largest tree-borne fruit, at almost 1 m (39 in) long, and can weigh up to 60 kg (132 lb). For decades, it has been grown for food, fuel, timber, medicinal extracts, and as a source of income for rural people [3,4]. Jackfruit is indigenous to the Western Ghats of southern India. Today, it is widely cultivated throughout the South and Southeast Asian region, the Caribbean, Latin America, and parts of Africa [5–7]. The latest WorldAtlas has recorded India as the world's top jackfruit producer, with 1.4 million tons produced, followed by Bangladesh, which claims jackfruit to be its national fruit, with 926 tons produced. Thailand and Indonesia are two other top jackfruit producers, with 392 and 340 metric tons, respectively (Figure 1) [8]. The jackfruit prices appear to have converged (below USD 1.00 per kg), except in areas of the world that are difficult to access, such as Australia (USD 2.91) and North America (USD 1.86) [9].

Jackfruit was listed under the National Key Economic Areas (NKEAs) as one of the economic-driven fruit crops of Malaysia, where its cultivation has been upgraded to a large scale [10]. The production value per metric ton was RM 1.25 in 2013, which increased

considerably to RM 1.60, RM 1.81, and RM 1.92 in the following consecutive years. In 2017 and 2018, the production value showed zero increments and remained static at RM 2.09. The harvested area decreased at that time from 3107 to 2979 Ha. It was then that outbreaks of jackfruit-bronzing were first reported in the country. Nearly 10,000 ha of jackfruit plantations were affected by the disease symptoms, with a 50–80% disease incidence. The production value of jackfruit then decreased to RM 1.95 and RM 1.88 in 2019 and 2020, respectively [11,12]. While this was happening, jackfruit production in the Philippines declined, falling from 47.09 metric tons in 2012 to 40.2 metric tons in 2020 [13].

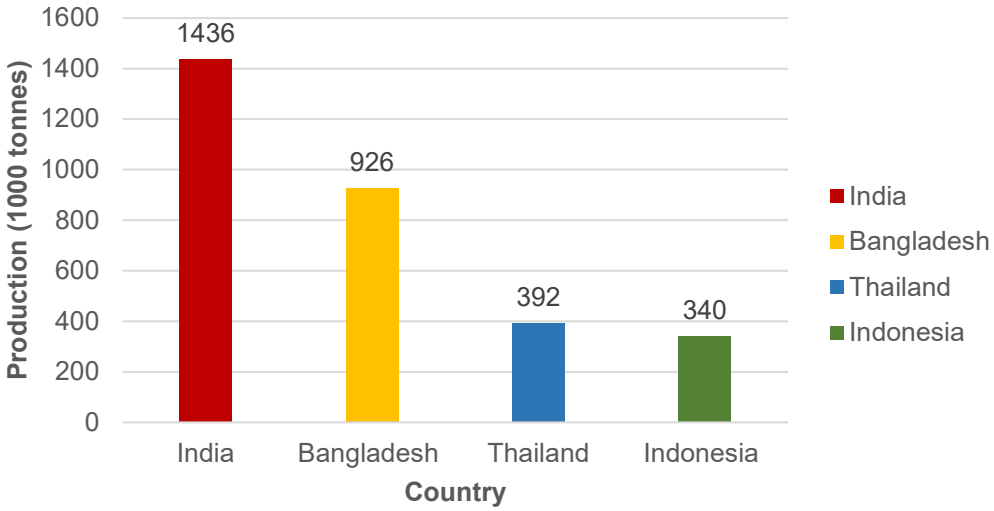


Figure 1. Top countries for jackfruit production. Data from [8].

Previously, as far as we knew, jackfruit had few disease problems; those we knew of were caused by bacterial and fungal infections and some nematode species. *P. stewartii* subsp. *stewartii* and *Dickeya fangzhongdai* are two prevalent bacterial pathogens that cause jackfruit-bronzing and fruit rot diseases [14]. However, most reported cases of issues with jackfruit in the past were fungal-causing diseases such as leaf spots, dieback, fruit rot, and pink disease caused by *Colletrotichum gloeosporioides*, *Phytophthora palmivora*, and *Rhizopus* sp. The diseases are commonly spread in orchards with poor air circulation or during wet seasons with high relative humidity and temperatures [15,16]. In India and China, the most common species infecting and parasitizing jackfruit trees were *Tylenchorhynchus mashhoodi* and root-knot nematodes *Meloidogyne enterolobii* [17–19]. These plant pathogens pose a significant threat to the plant productivity, yields, and long-term viability of plantations. Uncontrolled epidemic diseases resulting from such pathogens in the future might restrict the agriculture growth sector at domestic and international levels.

In Malaysia, jackfruit-bronzing was first reported in the plantation areas of Selangor and Pahang [20]. Indicated by yellowish to reddish discoloration on the affected fruit pulp and rags, the disease urgently threatens jackfruit industries. It has reduced the quality of fresh jackfruit and further afflicts jackfruit marketing economically [21,22]. Recently, a persistent onslaught of jackfruit-bronzing has significantly constrained jackfruit production, resulting in a massive loss of yield and further distracting the jackfruit growth sector.

A public review on jackfruit-bronzing was published by [23], focusing on the diagnostic approaches for *P. stewartii* subsp. *stewartii* in Malaysia, particularly its pathogenicity and genetic diversity, highlights polymerase chain reaction (PCR) amplification assay and multilocus sequencing analysis (MLSA). Despite little information on the commercialization value of jackfruit, limited information exists on the bacterial pathogen's virulence factors and genome sequence. There is merely one complete genome sequence of *P. stewartii* subsp. *stewartii* strain DC283 (GenBank Accession No: CP017581) is available in public databases.

This review provides an overview of recent research and advances in biology, diagnostics, pathogenomics, and potential disease management strategies of *P. stewartii* subsp.

stewartii's infection to improve the quality of local jackfruits. It is crucial to ensure the high quality and quantity of local jackfruit supplies to meet the increasing demand of domestic and international market needs.

2. Significance of Jackfruit-Bronzing Disease

Jackfruit-bronzing disease was first reported in the Philippines when the internal parts of the jackfruit changed to yellowish-orange and reddish discoloration. As a result, the quality of jackfruit dropped and disrupted the farmers-consumers supply chain. A research group [21] discovered a bacterium known as *P. stewartii* subsp. *stewartii* act as the disease's causal agent. Interestingly, this bacterium was the same pathogen causing Stewart's wilt on corn plants and localized lesions symptoms in pineapple (Figure 2).

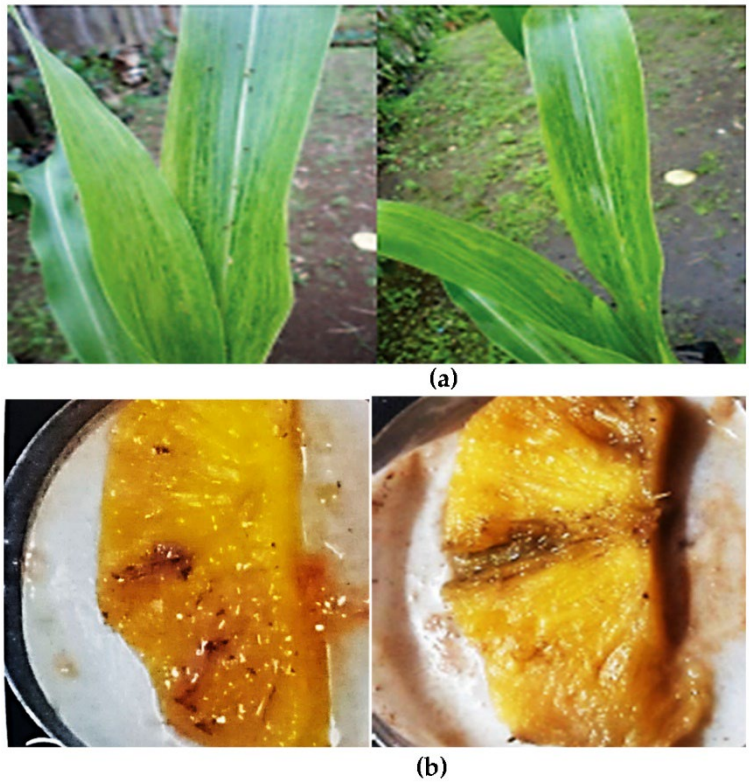


Figure 2. (**a**) Corn plant and (**b**) pineapple fruitlet inoculated with jackfruit-bronzing bacterium *P. stewartii* subsp. *stewartii* showing typical leaf blight symptoms and localized lesions [24]. Adapted with permission from [21].

This disease was reported in Malaysia three years later, where the bronzing symptoms appeared in the jackfruit plantations of Pahang state. This discovery ultimately answered the mystery of the rotting, rust, and rot-like symptoms previously discovered in plantation areas of Pahang and Negeri Sembilan state in 2010 [25]. The identified pathogen retained similar morphological and biochemical characteristics described by the Philippines research group. Species-specific PCR amplification confirmed *P. stewartii* subsp. *stewartii* as the causal agent of jackfruit-bronzing disease in Malaysia [20,26,27]. The disease later spread across North America when the fruit bronzing symptoms were observed in Nayarit jackfruit orchards, Mexico. The so-called 'Mexican bacterial isolates' matched the causal pathogen found earlier in the Philippines and Malaysia [22].

Typical fruit bronzing is a skin disorder of irregularly shaped patches marked by purplish or bronze-colored skin [28–30]. Unlike typical fruit bronzing, jackfruit-bronzing is associated with internal symptoms and can only be observed whenever the fruit is cut open. However, the plant pathologists indeed shared and highlighted the similar significant characteristics of these disease symptoms. Jackfruit-bronzing symptoms indicate rusty

and yellowish-orange to reddish discoloration of the affected pulps and rags (Figure 3). The symptoms primarily exist in sweetened jackfruit variety and higher brix composition, specifically the Tekam Yellow (J33) variety [2]. Once infected, the color of the internal parts is deviated from their original and is no longer attractive with the presence of bronzing specks all over the jackfruits pulps and rags.

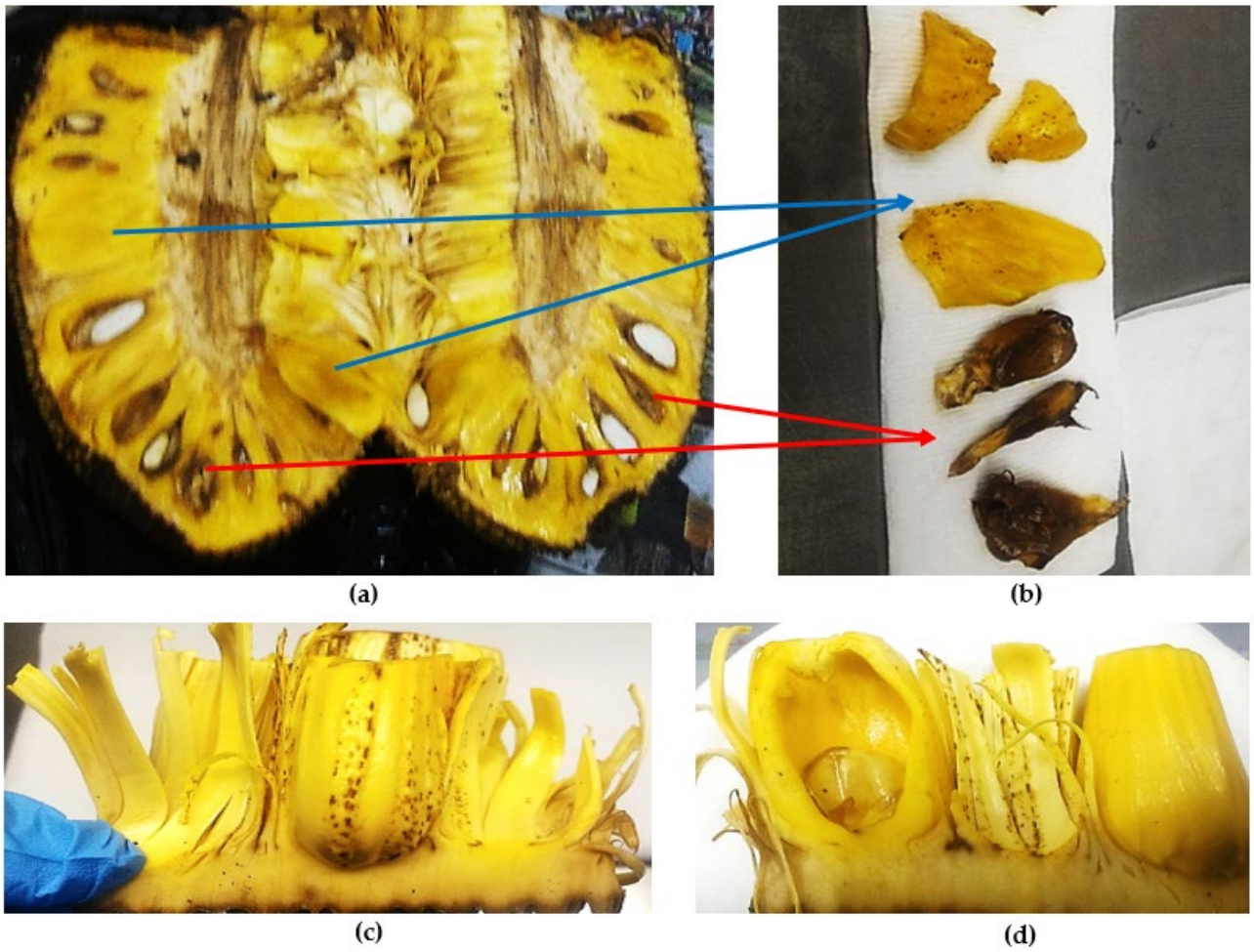


Figure 3. Symptoms of jackfruit-bronzing are present on the internal fruit parts. (**a**) Yellowish orange to reddish discoloration of the affected pulps and rags. (**b**) The pulps (blue arrows) and rags (red arrows) on clean tissues before isolation. The apparent brown specks symptoms on the infected (**c**) pulps and (**d**) rags (Figures were from personal collection).

3. *Pantoea stewartii* subspecies *stewartii*

3.1. History of Pantoea Species

The past five years' studies showed *P. stewartii, Pantoea ananatis,* and *Pantoea agglomerans* appeared as the top three's worldwide phytopathogenic *Pantoea* spp. inflicting damage and harming economically important crops and ornamental and flowering plant species. *P. stewartii* has been identified as the causal agent of leaf blotch on Sudan grass and Stewart's wilt on *Dracaena sanderiana* in California and South Korea [31,32]. Recent publications associated *P. stewartii* with bacterial leaf blight (BLB) of rice in Thailand and the West African countries of Benin and Togo [33–35].

Two subspecies were proposed under *P. stewartii* when [36] managed to differentiate *P. stewartii* subsp. *stewartiii* from *P. stewartii* subsp. *indologenes*. In opposite to *P. stewartii* subsp. *indologenes*, *P. stewartii* subsp. *stewartii* cannot produce indole, utilize citrate, grow on cis-aconitate, and form acid from carbohydrates. *P. stewartii* subsp. *stewartii* recognizes maize (*Zea mays*), sweet corn (*Zea mays* subsp. *mays*), teosinte (*Zea mays* subsp. *Mexicana*

and *Zea mays* subsp. *parviglumis*) as its main hosts [37]. Instead, the bacterium is known for causing Stewart's wilt or Stewart's bacterial wilt of maize and sweet corn, an economically significant disease affecting corn industries in Canada and the USA in the late 1980s [38,39]. A decade after, Stewart's wilt disease was detected in Argentina [40] and Bogor district in Indonesia [41].

Another subspecies, *P. stewartii* subsp. *indologenes* is a known pathogen of rot on pineapple *(Ananas comosus),* rot and leaf spot on foxtail millet *(Setaria italica),* as well as pearl millet *(Pennisetum americanum).* In addition, it is virulent against various plant hosts. For example, it is known as a new causative agent of rice (*Oryza sativa*) BLB disease [42,43], center rot of onion *(Allium cepa)* [44], and leaf blight wilt on a flowering plant species of *Asparagaceae*, the *D. sanderiana* [45]. Figure 4 illustrates the host plants and diseases caused by *P. stewartii* and its two subspecies; *P. stewartii* subsp. *indologenes* and *P. stewartii* subsp. *stewartii.*

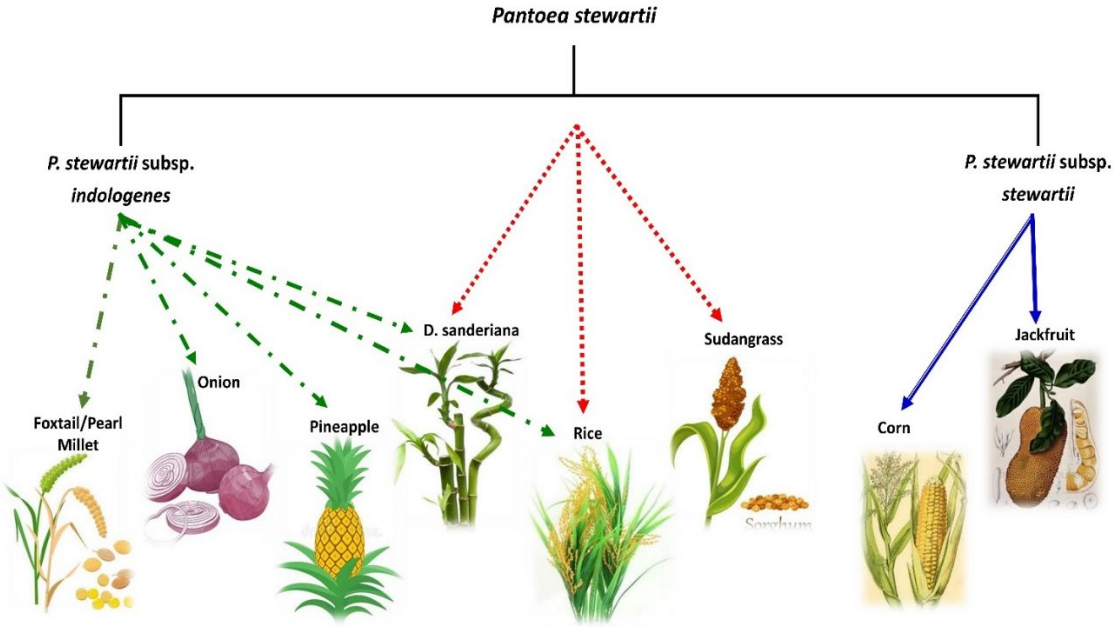
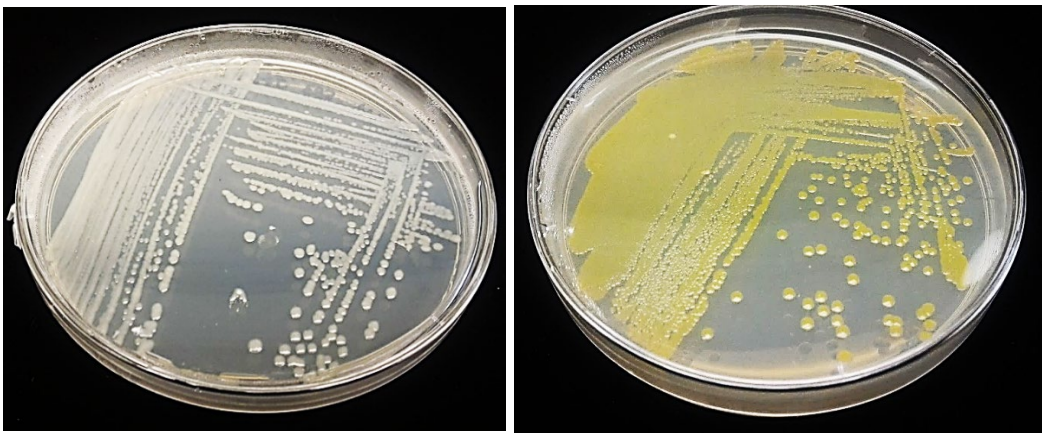


Figure 4. Host plants of the phytopathogens *P. stewartii*, *P. stewartii* subsp. *indologenes*, and *P. stewartii* subsp. *stewartii. Pantoea stewartii* (red dotted arrows) causes leaf blotch of Sudan grass, Stewart's wilt of *D. sanderiana* and BLB of rice (*O. sativa*); *P. stewartii* subsp. *indologenes* (green dotted arrows) causes rot of pineapple (*A. comosus*), leaf spot of millets (*S. italic* and *P. americanum*), center rot disease of onion (*A. cepa*), leaf blight wilt of *D. sanderiana* and BLB of rice (*O. sativa*); *P. stewartii* subsp. *stewartii* (blue arrows) causes Stewart's wilt of corn and bronzing disease of jackfruit (*A. heterophyllus*).

3.2. Biology

P. stewartii subsp. *stewartii* is a Gram-negative, facultatively anaerobic, non-flagellate, and rod-shaped bacterium. It taxonomically falls under Gamma-proteobacteria, order Enterobacteriales, family Erwiniaceae, genus *Pantoea*, and species *P. stewartii*. The colonies are creamy or pale yellow to lemon or orange-yellow, morphologically flat to convex, round with a 1–4 mm diameter, and translucent with a smooth margin on the King's B (KB) medium (Figure 5).

P. stewartii subsp. *stewartii* originated in the USA and is widely disseminated to Africa, North, Central and South America, Asia, and Europe [46]. A recent pest survey card by [47] reinforced *P. stewartii* subsp. *stewartii* as a Union Quarantine Pest and urged specific measures to prevent the introduction of this bacterium. At present, the corn flea beetle *(Chaetocnema pulicaria)* acts as the primary vector for the pathogen. At the same time, the European Union considered maize seeds the main pathway for introducing and spreading Stewart's wilt disease.



(**a**) (**b**)

Figure 5. (**a**) Creamy and (**b**) yellowish colony morphology of *P. stewartii* subsp. *stewartii* on a King's B agar medium isolated from jackfruit (*A. heterophyllus*) samples suffering from a bronzing disease in Malaysia (Figures were from personal collection).

The life cycle of *P. stewartii* subsp. *stewartii* associated with jackfruit-bronzing is yet to be discovered, and there is little information available on the etiology of this disease. However, jackfruit seeds may be a potential vector of the disease, seeing the propagation by direct seeding is still being practiced worldwide, apart from grafting and cuttings techniques [48]. Shoot borers, bark borers, mealy bugs, and scale insects are the prevalent insect pests linked to most jackfruit diseases [49]. A current review by [50] reported that trunk borer, shoot, and fruit borer as major common insect pests attacking jackfruit. In contrast, bud weevil, spittle bugs, bark-eating caterpillars, and aphids are considered minor insect pests of jackfruit.

4. Diagnostics of *Pantoea stewartii* subspecies *stewartii* from Diseased Jackfruit with Bronzing Symptoms

Identification of the *P. stewartii* subsp. *stewartii* can be conducted in two different methods; (i) phenotypic methods such as morphology, pathogenicity, or behavior, and (ii) molecular methods [51].

4.1. Phenotypic Characterization

Phenotypic characterization is a popular method due to low-price reagents and affordable equipment. This method allows the identification of the bacterial species from the genus up to the species level through the colony and cell morphology, Gram reaction, and metabolic and growth characteristics. Initially, a pure culture should be grown on media with various salt concentrations to identify the jackfruit-bronzing bacterium. Media such as 523, yeast dextrose carbonate, PA 20 [31,52,53], casamino acids peptone glucose [54], Luria-Bertani [22,55], and *Pantoea* genus-specific agar [56] are examples of media that serve for the purpose. Meanwhile, the King's B supplemented with nutrient-broth yeast extract agar or yeast peptone glucose agar has been applied as the selective media for the growth of *P. stewartii* subsp. *stewartii* at 25 to 28 °C [57].

Following the colony mentioned above and morphological identification, Gram-staining was performed to differentiate the *Pantoea* species under a compound light microscope with oil immersion lenses for a 100x magnification. Biochemical tests were carried out to determine the biochemical properties of the bacterium. Table 1 represents selected tests and outcomes for identifying the jackfruit-bronzing bacterium. Biochemical tests show that bacteria use carbon sources to obtain energy and sustain life. Therefore, the test outcomes on which carbon sources react allow for a probabilistic assessment [58].

Table 1. Phenotypic characterization *P. stewartii* subsp. *stewartii*.

Test	Outcome	Reference
Gram staining	(-) Gram-negative, short straight rods (0.4−0.7 × 0.9−1.7 µm)	[21,26,59]
Kovac's oxidase test	(-) No color change	
Capsule staining	(-) Non-capsulated	
Endospore staining	(-) Non-endospore former	
Motility	(-) Non-motility	
Tween80 hydrolysis	(-) No opaque haloes	
Acetoin and indole production	(-) No production	
Nitrate reduction	(-) No reduction	
Growth on cis-aconitate	(-) No growth	
Acid from carbohydrates	(-) Maltose, arbutin, salicin	
Catalase reaction	(+) Produce bubbles	
Oxygen requirement	(+) Facultative anaerobe	
Potato test	(+) Produce lesion or pit	
Starch hydrolysis	(+) Utilize starch in the medium	
Gelatin liquefaction	(+) Hydrolyze gelatin	
Tobacco hypersensitivity	(+) Necrosis of infiltrated tissues	
Acid from carbohydrates	(+) Glucose, galactose, fructose and sucrose, raffinose	

Hypersensitivity reaction (HR) is a quick and useful determinative test to discriminate plant pathogens from saprophytes by their capabilities to produce an HR in the leaf mesophyll tissue [60]. Essentially, a pathogenicity test should be carried out to confirm the infection by *P. stewartii* [59]. The test can be performed on healthy detached or attached jackfruit or jackfruit pulps [21,26,27]. The 10^8 CFU/mL bacterial inoculum is injected into the sterile and dried pulps and incubated in a controlled sterile chamber. Observation and examination for bronzing symptoms development are monitored daily for 2-weeks post-inoculation. The bacterial pathogen is reisolated and verified to identify the morphology, biochemical, and microscopic properties to confirm Koch's postulates. Although similar type symptoms were perceived in artificially inoculated jackfruits, the bronzing symptoms are relatively brighter than the naturally infected ones. It is most likely due to the different periods, considering the artificially inoculated fruits are cut open when it is still at an early stage. Disease incubation is longer in naturally infected jackfruits since the infection occurs earlier and longer than 2-weeks [21]. Therefore, different jackfruit varieties could be used to discover the most resistant and sensitive varieties to bronzing disease. The most recent publication investigated the pathogenic variability of *P. stewartii* subsp. *stewartii* infection against three different jackfruit varieties in Malaysia; Tekam Yellow (J33), Hong (J34), and Subang Chap Boy (J39) [24].

4.2. Molecular Characterization

The molecular methods are one of the primary identification tests for *P. stewartii* subsp. *stewartii* [59]. Besides serological tests and fatty acid profiling assay, the molecular approaches are applicable for phylogenetic and diversity analyses of prokaryotic taxa. The methods utilized two alternatives, either (i) hybridization of DNA–DNA homology to determine the relatedness of two microorganisms or (ii) sequencing of 16S ribosomal RNA (rRNA) to identify the bacterial species [58,61]. In addition, molecular methods can be further directed into PCR and barcoding.

4.2.1. Polymerase Chain Reaction

So far, rapid and sensitive PCR amplification targeting a single gene is generally used against *P. stewartii* subsp. *stewartii*-specific primers. The most-targeted gene regions for this bacterium are *cps* and *hrp*, responsible for pathogenicity and virulence. The *cps* gene cluster comprises 12 genes (cpsA to cpsM) that encode proteins to synthesize capsu-

lar polysaccharide (CPS) stewartan built up from seven monosaccharides repeating unit counting glucose, galactose, and glucuronic acid. On the other hand, the *hrp* gene encodes proteins for a type-III secretion system (T3SS) required for water-soaked lesions and general pathogenicity [54].

The most commonly used primers are (fD1; rD1) [62], (ES16; ESIG2c), (*cpsL1; cpsR2)*, and *(hrp1d; hrp3c)* [54] that target 16S rRNA and 16S-23S rRNA/internal transcribed spacer (ITS) partial gene sequences, *cpsD* and *hrpS*, correspondingly (Table 2). The *cpsD* and *hrpS* genes are chosen as targets as they appear unique to *P. stewartii* subsp. *stewartii.* DNA samples of infected jackfruit parts and ooze [21] can be used as templates, and the PCR program is set according to the manual procedure described by Coplin et al. [54]. After separation on an electrophoresed agarose gel (1%), amplification is observed at respective ~1.5 kb, ~0.92 kb, ~1.1 kb, and ~0.9 kb size amplicons. BLASTn and phylogenetic analyses will be conducted to see their similarities with *P. stewartii* subsp. *stewartii* reference strains in the GenBank databases.

Table 2. Primers and their sequences, targeted gene regions, and amplicon sizes used in single-plex PCR to identify the jackfruit-bronzing bacterium *P. stewartii* subsp. *stewartii*.

Primer Name	Primer Sequence (5′-3)	Target Gene	Amplicon Size (bp)	References
ES16	GCGAACTTGGC-AGAGAT	16S−23S rRNA/ITS	920	[20,21,26,54]
ESIG2c	GCGCTTGCGTGT-TATGAG			
*cpsL*1	CCTGTCAGTCTCGAACC	*cpsD*	1100	[21,22,27,54]
*cpsR*2	ATCTCGAACCGGTAACC			
*hrp*1d	GCACTCATTCCGACCAC	*hrpS*	900	[22,27,54]
*hrp*3c	GCGGCATACCTAACTCC			
fD1	AGAGTTTGATCCTGGCTCAG	16S rRNA	1500	[22,62]
rD1	AAGGAGGTGATCCAGCC			

4.2.2. Barcoding

Apart from PCR, barcoding is another molecular method to identify *P. stewartii* subsp. *stewartii.* EPPO recommended MLSA for a higher resolution of phylogenetic relationships of species within a genus or family [59]. It is an up-to-date method in prokaryotic taxonomy utilizing housekeeping genes or partial sequences of *gyrB* (encodes DNA gyrase subunit B), *rpoB* (encodes RNA polymerase beta subunit), *atpD* (encodes ATP synthase F1, β-subunit), and *infB* (encodes translation initiation factor IF-2) genes to build phylogenetic trees and deduce phylogenies [61]. A minimum of four genes are required in MLSA since a single gene would introduce bias and not reflect the general phylogenetic relationships other than the evolution of that single gene. Furthermore, MLSA deals precisely with internal fragments of four protein-coding genes at once (concatenated), reflecting the genuine phylogenetic relationship of bacterial taxa [63].

A recent report on the genetic diversity of *P. stewartii* subsp. *stewartii* isolated from jackfruit-bronzing samples was published by Abidin et al. [26], following the protocol described by Brady et al. [64]. Results were interpreted in two phylogenetic trees based on (i) single and (ii) concatenated *gyrB, rpoB, atpD,* and *infB* genes. Although phylogenetic trees based on a single gene scored maximum similarities (99% to 100%) between subspecies *stewartii* and *indologenes*, the concatenated genes-based phylogenetic tree is capable of pointing out the closer relation with *P. stewartii* subsp. *stewartii*, although the *P. stewartii* subsp. *indologenes* were in the same cluster. In a simple explanation, the *P. stewartii* subsp. *stewartii* strains from diseased jackfruits were polyphyletic in the 16S rRNA gene tree, thus forming a distinct monophyletic cluster in the MLSA analysis [65].

Essentially, the genus *Pantoea* is linked to the MLSA scheme to clarify the problematic taxonomic situation within the family Enterobacteriaceae due to some indistinguishable paraphyletic genera from 16S rRNA gene phylogeny. As a result, the former genera were amended, and different species were reclassified into new genera. All *Pantoea* strains were

involved in the massive analysis by referring to the DNA groups II, IV, and V [66]. A huge amendment was made to the genus *Pantoea,* by which new species were included and former species were reclassified. *Pantoea citrea*, *Pantoea punctata,* and *Pantoea terrea* were transferred to the genus *Tatumella* [67]. The scheme also brought in the *Pectobacterium cypripedii* to the genus *Pantoea* as *Pantoea cypripedii* [68].

5. Pathogenomics and Pathogenicity of *Pantoea stewartii* subspecies *stewartii*

For this review, two available reports of (i) the complete genome sequence of *P. stewartii* subsp. *stewartii* DC283 (NCBI Ref. No: CP017581.1) [55] and (ii) draft genome sequence of *P. stewartii* subsp. *stewartii* SQT1 (NCBI Ref. No: PRJEB36196) [69] were compared and further discussed (Table 3). The *P. stewartii* subsp. *stewartii* DC283 was isolated from the corn plant of the USA, which is associated with Stewarts' wilt disease. The genome size is 5,314,092 bp with 53.8% GC content, 5625 coding sequences (CDSs), and 100 RNAs. Meanwhile, *P. stewartii* subsp. *stewartii* strain SQT1 was isolated from Malaysian jackfruit suffering from a bronzing disease. The draft genome sequence is relatively shorter (4,783,993 bp long) with 67 contigs and contains less G+C content (53.7%), CDSs (4609), and RNAs (71). Rapid annotation using subsystem technology (RAST) has identified that 52% of genes fall into 27 active variants of subsystems. This review expanded the subsystem categories to the secondary metabolism to discover specific genes or gene clusters of pathogenicity and virulence of the jackfruit-bronzing pathogen.

Table 3. Genome features of the complete genome sequence of *P. stewartii* subsp. *stewartii* DC283 and draft genome sequence of *P. stewartii* subsp. *stewartii* SQT1.

Strain	Genome Features				
	Size (bp)	GC Content (%)	Coding Sequences	RNAs	Reference
P. stewartii subsp. *stewartii* DC283	5,314,092	53.8	5625	100	[55]
P. stewartii subsp. *stewartii* SQT1	4,783,993	53.7	4609	71	[69]

Based on pathogenicity and virulence of the *P. stewartii* subsp. *stewartii* DC283 strain, the T3SS of 'membrane transport' and exopolysaccharides (EPS) of 'cell wall and capsule' categories are the key pathogenicity factors contributing to Stewart's wilt disease developing symptoms [70], with an essential type-III effector protein from the AvrE family, WtsE. Other virulence factors, such as quorum sensing, biofilms, endoglucanase, cell-wall-degrading enzymes, and transcription factors, are necessary for successful colonization and infection of host tissue [71–73]. The T3SS is associated with the water-soaked formation during the wilt phase, while EPS is produced during the leaf blight phase and causes wilt seedlings, dry and necrotic leave lesions, and stunting and pitch rot mature corn plants [74,75]. The structure of EPS stewartan from the corn pathogen bacterium was published in 1990-ties [76,77], with high-molecular-weight (~1.4 MDa) heteropolysaccharide and over 1000 repeating units [78]. Furthermore, a fragile yet robust flagellar was one of the imperative characteristics of a bacterium that mediates its surface-based motility, which is essential for community development [70,79]. In comparison, ATP-binding cassette (ABC) transporter, type-VI secretion system (T6SS), and EPS are the main pathogenicity tools used by the *P. stewartii* subsp. *stewartii* SQT1 to deliver virulence factor into the host cells.

5.1. Membrane Transport: ATP-Binding Cassette Transporters and Type-VI Secretion System

Secretion of proteins across phospholipid membranes is one of the essential component strategies for many bacterial pathogens to invade susceptible hosts and promote virulence. They primarily draw attachment to eukaryotic cells, scavenge resources in an environmental niche, intoxicate target cells and disrupt their functions. The largest and most diversified superfamily, ABC transporters, play a pivotal role in bacterial pathogenicity and cell survival for the *P. stewartii* subsp. *stewartii* SQT1. The ABC transport system

comprises three proteins transporting substrates across cellular membranes using ATP binding and hydrolysis [80–82]. Two main transporter subgroups (importer and exporters) mediate the uptake of nutrients into the cell and extrude toxins and drugs. The third subgroup involves diverse cell functions [83]. Rather than saprophytes or animal pathogens, ABC transporter homologs are abundant in phytobacterial pathogens, strengthening their importance for pathogenesis.

The soft rot *Pectobacteriaceae* and *Agrobacterium tumefaciens* encode approximately 80 and 160 ABC transporters per genome [84], while the *P. stewartii* subsp. *stewartii* SQT1 encodes an average of 46 ABC transporters. The genera Pectobacterium and Pantoea are members of the order Enterobacterales, which is well-known for producing agriculturally harmful phytopathogens (Figure 6). Dipeptide permease (*Dpp*) is the major peptide transporter detected, followed by oligopeptide permease (*Opp*). Branched-chain amino acid (*Liv*) and alkyl phosphonate (*phn*) are the least peptide transporters in the genome. The peptide transport systems are commonly used to import peptides for nutrient sources and get cellular function signals [81]. The detection of dipeptide permease (*DppABCDF*) and oligopeptide permease (*OppABCF*) systems is comparable with two hetero-oligomeric oligopeptide transporters found in *Escherichia coli* [85], yet *E. coli* uses *Opp* as the core peptide transport system.

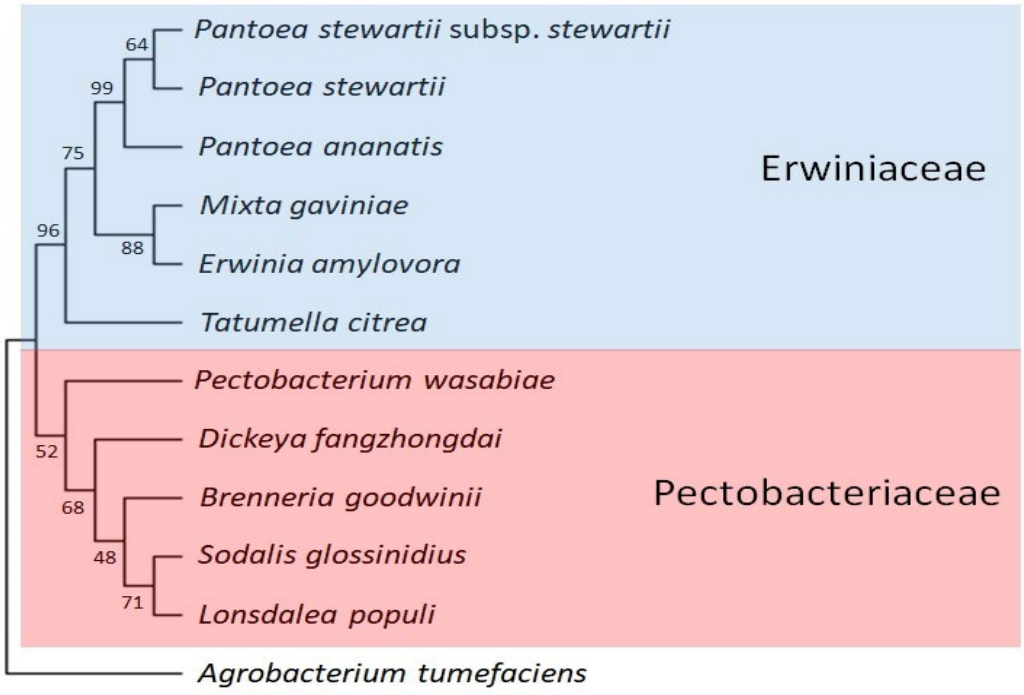


Figure 6. The phylogenomic tree depicted typical strains of Erwiniaceae and Pactobacteriaceae within the order Enterobacterales. The order is well-known as agriculture-harming phytopathogens, predominantly the genera *Pantoea*, *Erwinia* (Erwiniaceae), *Pectobacterium, Dickeya, and Brenneria* (Pectobacteriaceae). These clades include the species of the genera *Mixta, Tatumella, Sodalis*, and *Lonsdalea*. The causal agent of crown gall disease, *Agrobacterium tumefaciens* is an outgroup.

The mechanisms driving these events are never adequately elucidated, and information on the regulatory network of bacterial peptide transporters involved in pathogenesis is limited. Figure 7 shows the key inducer for peptide transporter expression and the principal bacterial virulence-associated with peptide transporters [81,82,86,87].

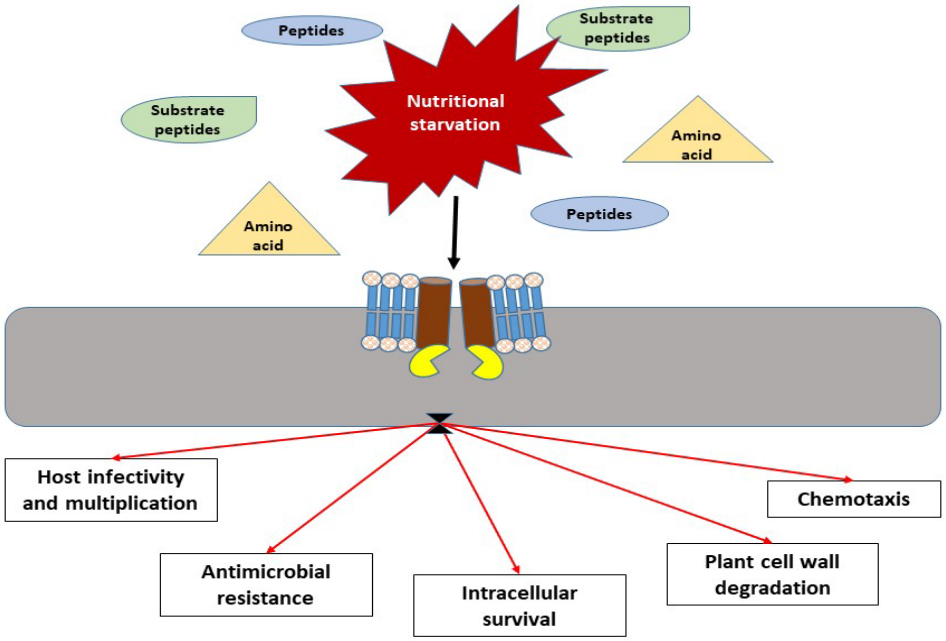


Figure 7. ABC peptide transporters use the nutritional starvation condition as the main inducer for their expression, which leads to major bacterial virulence such as plant cell wall degradation, chemotaxis, intracellular survival, antimicrobial resistance, infectivity, and multiplication in host plants (red arrows). The mechanisms involving component systems regulating the expression of peptide transporters are not included in this diagram.

T6SS is another central protein secretion system in the 'membrane transport' category despite ABC transporters. T6SS is a complex structure composed of 13 to 15 proteins conserved in all T6SS clusters across species of Gram-negative bacteria [88–91]. T6SS is critical in delivering toxins into eukaryotic and prokaryotic cells, either host or competitors [89–91], and is always referred to as nanomachine. Horizontal gene transfer is the leading way of T6SS traits acquisition and is not the standard duplication [92]. Many studies have reported the implication of T6SS in virulence by modifying the cytoskeleton of the eukaryotic host and in broad, violent, and purposeful inter-bacterial competition to prevent the growth of rival cells [93–95]. Bacterial pathogens mediate virulence into neighboring bacteria to compete for a specific host niche [96–100], particularly the space and resources [101]. These toxins are crucial for significant fitness during host colonization as they generate immunity proteins to avoid self-intoxication or being targeted by sister cells [95,101,102]. The secretion system is distributed intoT6SS-I, T6SS-II, and T6SS-III, which are directly involved in respective cell subversion/pathogenesis, virulence, and bacterial competition [103].

Based on subsystem feature counts on the RAST seed viewer, the *P. stewartii* subsp. *stewartii* SQT1 consists of 18 of 27 T6SS genes (Figure 8) and half encodes proteins with unknown functions. VgrG (valine-glycine-repeats G) appears to be this genome's most plausible secreted protein. T6SS secreted the VgrG protein in *Vibrio cholera* and Hcp (hemolysin co-regulated protein) [104]. Hcp structurally creates hexameric rings with a central channel surrounding the VgrG tube. The VgrG punctures the outer cell membrane, allowing the Hcp tube to extrude and consequently breach the host cell membrane to transport the effectors/toxins into target cells. These proteins are notably essential components of the system and substrates of the T6SS [105].

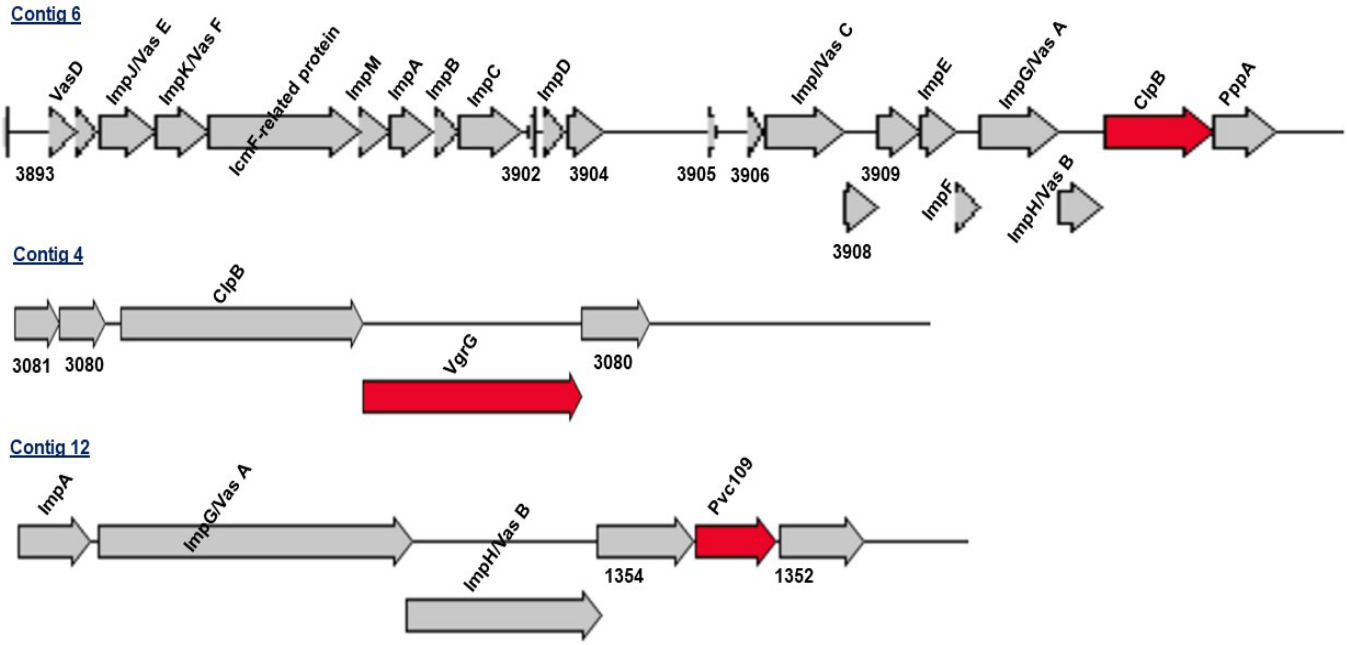


Figure 8. Genetic organization of 18 annotated T6SS gene clusters in *P. stewartii* subsp. *stewartii* SQT1; Contig 6 (*VasD*, *ImpJ/Vas E*, *ImpK/Vas F*, *IcmF-related protein*, *ImpM*, *ImpA*, *ImpB*, *ImpC*, *ImpD*, *ImpI/Vas C*, *ImpE*, *ImpF*, *ImpG/Vas A*, *ImpH/Vas B*, *ClpB*); contig 4 (*ClpB*, *VgrG*); contig 12 (*ImpA*, *ImpG/Vas A*, *ImpH/Vas B*, *Pvc109*). PppA, *ImpA*, *ImpG/Vas A*, and *ImpH/Vas B* are found on contig 6 and contig 12, while *ClpB* is found on contig 6 and 4.

Another significant gene, *icmF* (intracellular multiplication F), was identified in the T6SSs of *P. stewartii* subsp. *stewartii* SQT1. The *icmF* was previously reported on the inner membrane of *Legionella pneumophila* and located downstream of *dotU* (defect in organelle trafficking U) gene [89,106]. Many studies suggested that both *icmF* and *dotU* may work together and interact in assisting the assembly and stability of a functional *dot–icm* complex [107–110] and are even required for virulence [111,112]. These genes are the only T6SS components with transmembrane domains that render a membrane channel traversing the bacterial cell envelope [89,102]. The *dotU* was not observed in the draft genome sequence; however, two *dotU* homologs were found; *impK* (impaired in nodulation K) and *vasF* (virulence associate secretion F), each encoded by *imp* and *vas* clusters. The outer membrane (OM) ImpK protein-coding gene is among eight genes encoding proteins with unknown functions (ImpA, ImpB, ImpC, ImpD, ImpF, ImpH, ImpI, ImpJ), and three other genes encode for avirulence locus ImpE protein, ImpG protein, and phosphatase ImpM protein. The *imp* are homologous to *vas* and encode related proteins [113]. ImpG protein had homology with VasA, while uncharacterized proteins ImpH, ImpI, and ImpJ are homologous to VasB, VasC, and VasE. A *vasD* gene encoding type-VI secretion lipoprotein is also present, but not the *vasH* (sigma-54 dependent transcriptional regulator), *vasI* (type VI secretion protein) and *vasL* (type-VI secretion-related protein). The *vas* system is required for secreting proteins lacking an N-terminal signal peptide and has no effects on proteins with signal peptides such as chitinase and neuraminidase [89,104].

clpB (caseinolytic peptidase B) and *pvc109* (pyoverdine chromophore 109) are other T6SSs spotted in the draft genome sequence. The Clp family belongs to the AAA+ superfamily of ATPases [114]. They form ring-shaped oligomers necessary for their ATPase activities and mode of action, particularly for macromolecular structural disruption [115,116]. A homolog of *clpB*, *clpV* is considered one of the core components of T6SS and acts as the T6SS motor [117,118]. Meanwhile, uncharacterized Pvc109 protein is similar to VCA109 and functions as a base plate assembly protein [119]. Significant gene cluster *pppA* encoding Ser/Thr phosphatases was also detected. The *pppA* is located next to the *clpB* on the contig 6, but *ppKA* encoding Ser/Thr kinases was not found. Both *pppA* and *ppkA* were encoded in the

first cluster, HIS-I (Hcp1 secretion island I) of *P. aeruginosa*. Yet in a second cluster (HIS-II), *stk* and *stp* genes were discovered to have similar encoding functions as *ppkA* and *pppA*. The PpkA and PppA work antagonistically in regulating Hcp1 secretion [120].

The T6SS complex also revealed the presence of *fha* encoding a protein with an FHA (forkhead-associated) domain, which is known to have an affinity for phosphothreonine [121,122]. Several studies have found a link between *fha1* and HCP1 secretion and its phosphorylation is associated with PpkA and PppA. The Fha phosphorylation may initiate a signal transduction cascade that leads to T6SS assembly and function [120]. However, not every T6SS gene cluster possesses the PpkA/PppA/Fha1 complex at the post-translational level, with some having only part of it and others having none.

E. amylovora and *P. ananatis* are the close relative of the *P. stewartii* subsp. *stewartii* to illustrate the macromolecular machines of T6SS [88] in virulence mechanism and interbacterial competition [91]. During disease interactions of *E. amylovora* with its plant host, T6SSs have altered metabolic and motility processes, and most importantly, they impacted the disease's progression [123]. While in *P. ananatis*, a compromised virulence phenotype was observed due to the incapability of the T6SS mutant to cause disease in onion *(A. cepa)* plants [124].

Following ABC transporter and T6SS are the type-II, -IV, and -V secretion systems. The T2SSs and T5SSs secrete proteins in two steps: (i) Sec/Tat secretion pathways and (ii) second secretion pathway. Meanwhile, T4SS is a Sec/Tat-independent and transport substrate across both bacterial membranes in a single step, resembling the T6SS [125].

5.2. Cell Wall and Capsule: Capsular- and Exopolysaccharides

CPS and EPS gene clusters suggest the active production of EPS stewartan from *P. stewartii* subsp. *stewartii* SQT1. Gram-negative bacteria are naturally covered in a surface-bound polysaccharide layer or capsule for protection against recognition by plant defense mechanisms, bind water to moisten the bacteria, and retain nutrients and ions released from damaged plant cells. These circumstances create a favorable environment for bacterial multiplication, aids the bacterial dissemination through plant tissues, and develop the characteristic symptoms of infection [126]. The CPS is released and free from the cell surface molecules as free EPS in certain circumstances, thus explaining the slime-forming or mucoid trait of many bacterial species (Figure 9) [127,128]. EPS is the primary pathogenicity factor for *P. stewartii* subsp. *stewartii* [70,129] and plays a vital role in bacterial survival and persistence, particularly in cell aggregation, cell adhesion, biofilm formation, and protection from hostile environments [128–131]. These acidic complex EPSs mask pathogens' recognition through plant defense reactions and promote bacterial growth and movement *in planta* [132].

EPS biosynthesis is similar to the Wzy-dependent pathway of O-antigens and groups 1 and 4 of CPS [133,134]. None of the O-antigen flippase, Wzx (related to MurJ of peptidoglycan assembly), or oligosaccharide repeat unit polymerase (Wzy) existed in the *P. stewartii* subsp. *stewartii* SQT1 genome exports the LPS across the plasma membrane to the periplasmic space. Interestingly, the detection of OM lipoprotein carrier protein (LolA), OM protein (YaeT), and four lipoproteins (YfgL, YfiO, NlpB and SmpA) suggested the involvement of the Lol system in transporting LPS to the OM (Figure S1) [135,136].

A set of polysaccharides export lipoprotein (Wza), low molecular weight protein-tyrosine-phosphatase (Wzb), and tyrosine-protein kinase (Wzc) were later discovered. The Wza and Wzb typically span the periplasmic space and promote the export of EPS polymer. The Wzb alone helps support the oligomerization of dephosphorylated Wzc with its phosphatase activity [137–139]. The remaining two proteins found in *P. stewartii* subsp. *stewartii* SQT1 was a putative CPS transport protein (YegH) and a putative uncharacterized protein (YmcB).

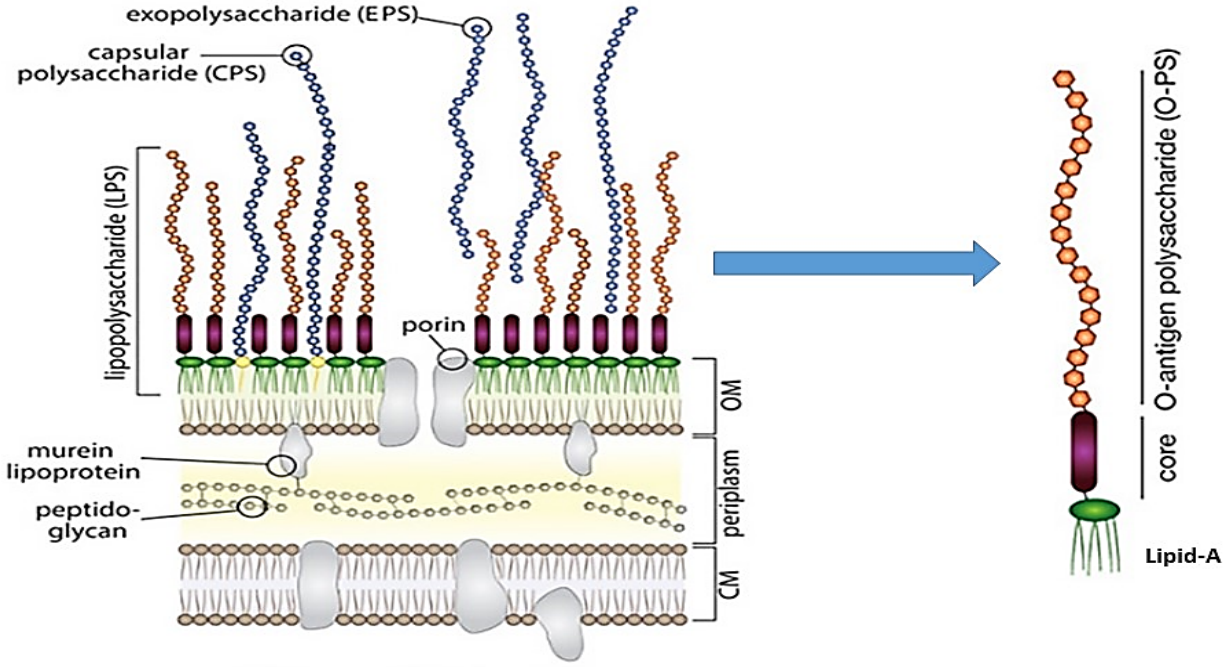


Figure 9. Conceptual organization of the cell envelopes of Gram-negative bacteria. An outer leaflet of the asymmetric OM is composed of LPS essential for the permeability barrier's integrity. LPS structure (blue arrow) is composed of lipid A and core oligosaccharides capped with a long O-antigen polysaccharide chain. The bacteria are covered in a CPS layer; at times, this CPS is released from the cell in large amounts as free EPS. Adapted with permission from [128]. Copyright © 2022, The Consortium of Glycobiology Editors, La Jolla, California.

CPS and O-antigen are critical components of cell walls and have been recognized as significant pathogenic factors in pathogenic bacteria [140]. CPS is best known for pathogenesis, yet it is intricate in promoting bacteria adherence to host organisms, facilitating biofilm formation, and conferring resistance to host innate immunity [141]. The O-antigen is the outer surface of lipopolysaccharide (LPS) and is built up together with lipid A (endotoxin) and core oligosaccharide (shown in Figure 9). There is abundant literature defining the association of the O-antigen with bacterial virulence in humans, animals, and plants [142–146].

6. Potential Mitigation Strategies for Jackfruit-Bronzing Disease

The peak incidences of jackfruit-bronzing were reported after or during the rainy season when the humidity ratio is relatively high. Healthy jackfruit trees are more tolerant to this disease, while stressed trees, mostly of nutrition imbalances, soil types, terrain conditions, and injury, are more vulnerable [25]. Therefore, adequate fertilization levels should be well maintained, concerning calcium and potassium, but not nitrogen and phosphorus. Excess soil moisture should be avoided to prevent the susceptibility of jackfruit trees to bronzing disease [147]. Cultural practices and chemical control are powerful mitigation strategies that could be integrated into managing the jackfruit-bronzing disease (Figure 10).

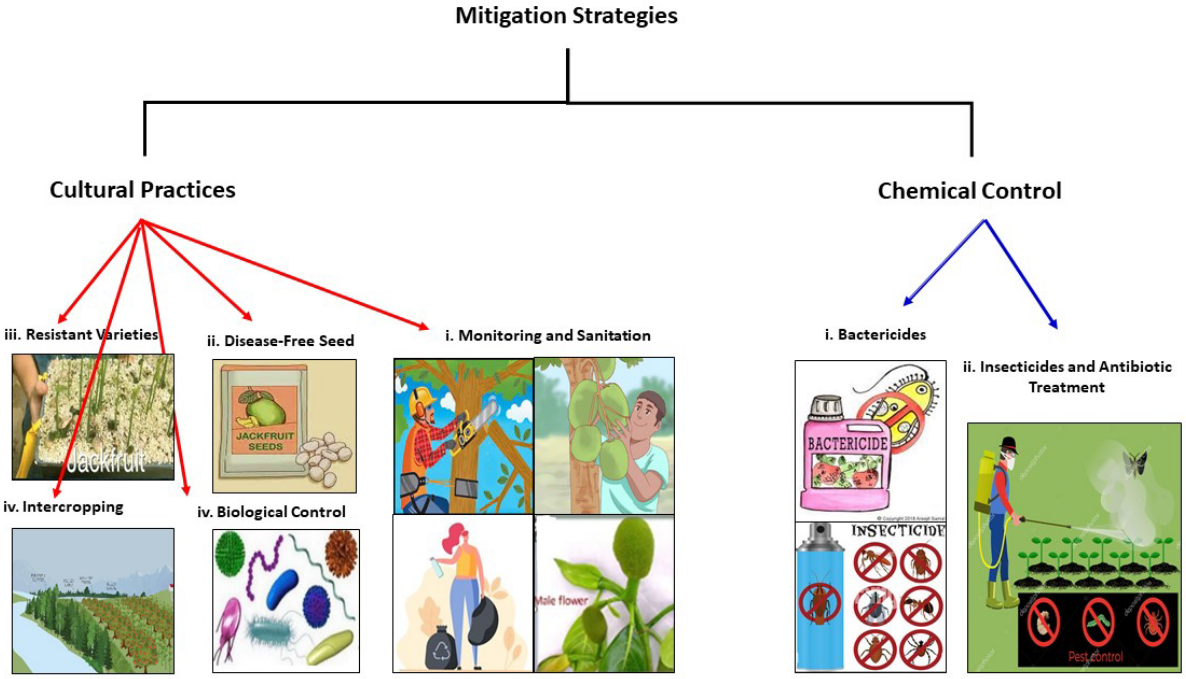


Figure 10. Potential mitigation strategies of jackfruit-bronzing disease. Cultural practices include monitoring and sanitation, disease-free seed, resistant varieties, biological control, and intercropping (red arrows). Chemical control includes bactericides, insecticides, and antibiotic treatment (blue arrows).

6.1. Cultural Practices

6.1.1. Monitoring and Sanitation

Jackfruit-bronzing attacks the fruit's internal part, and the visual symptom can only be seen when the fruit is cut open. Continuous monitoring of the incidence could be practiced in commercial growing areas by checking on the male inflorescence and internal fruit symptoms by inspecting the peduncle [25]. Direct monitoring, such as eradicating the infected trees, is necessary and should be at the forefront of management control. It is recommended that jackfruits be inspected at regular intervals of two weeks from each tree in the jackfruit plantation. Considering environment factors, clone types, tree age, and entry point of the pathogen, one month or longer monitoring intervals may practically apply. In certain areas where bacterial diseases are already present, immediate control should be taken in limiting any access into and out of the infected plantation, whether humans, animals, or any tools and equipment [148]. Destroying diseased fruits, disinfecting and sanitizing the suspected trees and their surroundings, pruning the low branches, and restricting the number of fruits are such practices that should be implemented. All actions must be done cautiously to avoid any wounds or injuries, particularly to the developing jackfruits.

Additionally, a shallow waterway could be built around the infected tree to drain superficial liquid or water-containing bacterial inoculum to limit bacterial dispersal. If the bacterial is spread to the secondary host trees, the male inflorescence's de-budding process should be performed in an instance. Finally, infected wrapping bags should be disinfected and removed from the plantation areas. While in disease-free areas, it is a must to avoid the entry of the causal pathogen by practicing reasonable sanitation procedures and using clean and sanitized planting tools and materials [149].

6.1.2. Disease-Free Seeds

The disease may potentially be transmitted by infected plant material and infected seeds. A disease-free seed from a certified source is the best choice to prevent the spread of

the bronzing disease. The certified seed is generally handled under procedures acceptable to the Department of Agriculture (DOA) and Forestry to maintain good genetic purity and identity [150]. The disease-free seed needs to be produced in areas where the disease is absent not to introduce the disease. If the seed is infected following the visual inspections for symptoms, an ELISA-based seed health test could be performed for confirmation. At the same time, regular inspections should be carried out on seed parent plants and the jackfruit growing field [151].

6.1.3. Resistant Varieties

Besides the disease-free seeds, jackfruit-resistant varieties are another imperative prevention strategy that commercial jackfruit growers may apply. In North America, planting resistant varieties (C123) has effectively controlled Stewart's wilt disease, which is caused by the same causal pathogen [152]. The disease resistance gene is inherited and shown in four inbred lines of dent corn by quantitative and qualitative analyses [153]. In Malaysia, there are a total of 15 jackfruit varieties; J2, J27, J28, J29, J30, J31 (NS1), J32 (Mantin), J33 (Tekam Yellow), J34 (Hong), J35 (Crystal Jackfruit 1), J36 (Crystal Jackfruit 6), J37 (Mastura), J38 (Subang Lao Zhang), J39 (Subang Chap Boy) and J40 (CJ3) registered for the national crop list [154]. A recent publication has reported the jackfruit variety J39 was the most resistant to the bronzing disease. Meanwhile, variety J34 was most susceptible to the disease [24] with sweet pulps and nearly 15% brix composition. Choosing the jackfruits with much less flavor variety and a low brix may help thwart the incidence of jackfruit-bronzing disease composition [2,21,23].

6.1.4. Biological Control

The biological control method is one of the sound and effective means to control the growth of *P. stewartii* subsp. *stewartii*. No biological agents are available to inhibit or mitigate bacterial infection [151]. Forty years back, there was an effort to isolate a bacteriophage of *P. stewartii* subsp. *stewartii* from *C. pulicaria* and characterize it according to the host range. However, it has not been developed adequately enough to be used [155]. Only eight of the 13 pathogen strains were tested, partially completed phage characterization. It was hypothesized that virulent bacteriophages might efficiently eliminate *P. stewartii* subsp. *stewartii* inside its beetle vector under field settings, but no further assertions or additional discussion was uncovered from the research effort.

6.1.5. Intercropping

Intercropping may be enforced to combat the risk of jackfruit-bronzing and weeds and insects [156,157]. Comparatively, intercrops are more effective in utilizing light, water, and nutrients, making a lesser amount available to weeds. In addition, intercrops reduce the number of susceptible hosts by acting as a physical barrier to the susceptible or host plants [158,159]. In this way, the diversity of pests and diseases is enlarged, thus plummeting the speed of pest adaption. Jackfruit and eggplant perhaps could be grown for the intercropping system [160] or jackfruit and pineapple [161], or jackfruit, pineapple, and aroid plant [162]. People in Bangladesh are used to the agroforestry cropping system, whereby more than one crop is planted in proximity for productivity, yield stability, and profit. The concept of multispecies systems has been practiced for decades [163]. The systems may include annual and perennial crops on a gradient of complexity from 2 species to more. Intercropping offers benefits such as upgraded soil health, decreased non-point source pollution by lowering nitrogen losses, excellent overall production, enhanced pest and disease control, enhanced ecological services, increased economic profitability, and improved ecological services.

The systems provide benefits such as increased overall productivity, better pest and disease control, improved ecological services, increased economic profitability, improved soil health, and reduce non-point source pollution by reducing nitrogen losses [164].

6.2. Chemical Control

6.2.1. Bactericides

Chemical control using copper-based bactericides is one of the imperative mitigation strategies for the jackfruit-bronzing disease proposed by the DOA of Malaysia [25]. Copper is essential for normal plant development and growth [165,166]. However, it is harmful to cells at high doses as it could disrupt the enzyme active sites, interfere with the energy transport system, and compromise the integrity of cell membranes [167]. The copper sprays must be applied evenly to the jackfruit surface before the disease infections. The copper starts functioning by water on the jackfruit's surface, forming exudates that weaken the acids and lower the pH. The solubility increases the dissolving and releasing of copper ions. When it comes into contact with bacteria, the ions make entry into the cell walls and disrupt the cellular enzyme activity. This bactericide spray is more effective yet less toxic by applying it frequently at low rates rather than infrequent applications at high rates. The fruit temperatures are low, humidity is low, and the fruit is not wet [168]. A relative of *P. stewartii* subsp. *stewartii*, *P ananatis* has shown sensitivity towards copper compounds and was relatively effective with copper bactericides to control the center rot disease of onion *(A. cepa)* [169,170]. In particular, the copper prophylactic sprays have shown excellent efficacy in preventing plant diseases caused by *Xanthomonas* spp., such as canker and bacterial spot of citrus [171], the bacterial blight of walnut *(Juglans*) [172], leaf blight of onion (*A. cepa*) [173], the bacterial spot in pepper *(Capsicum*) and bell pepper (*Capsicum annuum Group*) [174,175], bacterial spot and bacterial speck of tomato (*Solanum lycopersicum* L.) [176] and many more. In Nepal, the copper prophylactic spray has been effective against greening and canker of citrus, black rot of crucifers (*Brassicaceae*), and bacterial leaf spot of pumpkin (*Cucurbita moschata*)diseases [177]. On the other hand, long-term usage of copper may result in copper-resistant bacterial strains, making disease management more difficult. Once the targeted plant pathogen acquires resistance genes, the frequency of resistant strains in the pathogen population rapidly increases, and subsequent applications become less effective in disease management [178].

6.2.2. Insecticide and Antibiotic Treatment

Both insecticide and antibiotic treatments have been applied to control *P. stewartii* subsp. *stewartii* on corn crop mainly in the US and some parts of Indonesia. Clothianidin, imidacloprid, and thiamethoxam are systemic insecticides reported to lower systemic infection by up to 85% [179–182]. Unlike insecticides used in-furrow at planting or applied as foliar treatments, antibiotics have only been studied *in vitro*. Antibiotic treatment can be applied to the short-lived jackfruit seeds for 30 days. To defend jackfruits from infection before the bacterium is transmitted [183–185]. Xinzhimeisu (the mixture of Streptomycin and Terramycin), Wuyijunsu *(Streptomyces ahygroscopicus* var. *wuyiensis)* and Zhongshengjunsu (antibiotic 120) are several antibiotics that used to treat the corn seeds from *P. stewartii* subsp. *stewartii* infection [186]. Antibiotics-seeds soaking technique at the optimum temperature of 40 °C to 47 °C for 90 min can destroy the bacterium pathogen and stimulate the seed germination [187].

7. Conclusions and Future Prospects

Jackfruit-bronzing disease is a recent trending threat to the jackfruit industries in Southeast Asia. Uncontrolled spread may weaken the enthusiasm of jackfruit growers and diminish the jackfruit plantation areas. In Malaysia, the DOA has reported that the planted areas of jackfruit cultivation significantly reduced from 6245 to 4900 Ha from 2015 to 2018, reducing the harvested area from 3220 to 2980 Ha. In 2020, the plantation areas were reduced to 4675 Ha and maintained the same hectares in 2021. In line with the increasing population, sustainable jackfruit production needs to be secured to meet domestic and foreign demands. Moreover, further research is required to understand the pathogen's nature and pathogenicity better.

Single-plex PCR targeting a single gene is the primary technique to identify *P. stewartii* subsp. *stewartii* from symptomatic jackfruit either by using the universal 16S rRNA and 16S rRNA ITS primers or housekeeping genes (e.g., *gyrB*, *atpD*, *infB*, and *rpoB)* that are conserved in the genus and unique to each lineage, or subspecies-specific primers (e.g., *hrp* and *cps*) in narrowing down to the subspecies level. The amplified band sizes are expected at 0.9 kb to 1.5 kb on the electrophoresed gel. The diagnostic procedure proceeds with DNA sequencing and gene sequence analysis (BLASTn) before depositing into the GenBank. To gain information on the *P. stewartii* subsp. *stewartii's* evolutionary relationships, phylogenetic analysis is performed to analyze the genetic differences. More recently, multiplex PCR, loop-mediated isothermal amplification (LAMP), and quantitative PCR have been applied for multi-detection and the random detection of target sequences for large-scale studies to balance the needs, cost, and handling time.

Insights into the pathogen genome have shown that CPS and EPS as *P. stewartii* subsp. *stewartii*'s core pathogenicity factors in disease infection. Besides, the *Dpp and Opp* have been discovered as the significant peptide of ABC transporters in virulence. Hence, there is a possibility that these two may not be the primary peptide transporters for the pathogen, the *TPP*, or any other mode of transportation that requires more evidence from in-depth experimental trials. The genomes of wild-type and mutant strains of *P. stewartii* subsp. *stewartii* SQT1 must also be investigated in host plants, as the precise T6SS effectors are currently unknown. This genomic information is vital to determine the sources and patterns of transmission during specific disease outbreaks and to revolutionize infectious disease epidemiology research. At the same time, it helps to understand the correlation between taxonomy and mechanisms of virulence imposed by this pathogen and scrutinize new environmentally-friendly control strategies further to combat the jackfruit-bronzing disease globally.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae8080702/s1, Figure S1: Lipoprotein transport through the bacterial cell envelope. Following transport through the Sec system, the OM protein (YaeT) and four lipoproteins (YfgL, YfiO, NlpB, and SmpA) form a complex essential for OM protein biogenesis [136].

Author Contributions: R.I.: conceptualization, original draft preparation, and editing. S.I.I., M.Y.I.-S. and D.Z.: manuscript reviewing. S.I.I. and M.Y.I.-S.: supervision. D.Z.: project administration and supervision. All authors have read and agreed to the published version of the manuscript.

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