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Recent Progress in the Understanding of Citrus Huanglongbing: From the Perspective of Pathogen and Citrus Host

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Abstract: *Citrus Huanglongbing (HLB), or citrus greening disease, caused by the phloem-restricted bacterium Candidatus Liberibacter asiaticus (CLas) and transmitted primarily by the Asian citrus psyllid (Diaphorina citri), remains one of the most devastating threats to global citrus production, with no definitive cure. This review synthesizes recent advancements in* *understanding HLB from dual perspectives: the pathogen, focusing on genomics, effectors, virulence factors, transmission dynamics, and detection methods; and the citrus host, emphasizing perception and signaling, metabolic disruptions (starch accumulation, callose deposition, and source-sink imbalances), defense responses, and tolerance mechanisms in resistant varieties and relatives. Integrated insights highlight pathogen-host interactions, including effector-mediated suppression of plant immunity and multi-omics approaches like dual RNA-seq for elucidating molecular dialogues. Management strategies encompass vector control, sanitation, breeding for resistance via CRISPR genome editing, RNA interference, antimicrobial peptides, microbiome engineering, and nutritional therapies. Challenges such as CLas uncultivability and knowledge gaps in functional genetics are discussed, alongside future directions for early detection innovations, sustainable interventions, and multi-omics breeding pipelines to enhance citrus resilience.*

Keywords: Candidatus Liberibacter, CRISPR, Citrus Huanglongbing, IPM, RNAi-Based Control

1. Introduction

Citrus Huanglongbing (HLB), or citrus greening disease, is considered as one of the most destructive citrus diseases in the world as it affects citrus production greatly and has not been cured yet. The bacteria of the genus *Candidatus Liberibacter asiaticus* (CLas), cause this disease and are mostly transmitted by Asian citrus psyllid vectors (*Diaphorina citri* and *Trioza erytreae*) but also can be transmitted via infected budwood. Multiple recent research studies and advancements in disease knowledge complicate and intensify the problem of HLB (Zou et al., 2029).

HLB has negatively affected citrus industries around the world by lowering the productivity and quality of fruits, upsurge the costs of production following the adoption of strict control measures (Da Graça *et al*., 2015). The Patho system of HLB is extremely complicated with complex interactions between the citrus host, the pathogen and the vector. Metabolic pathways of the host plant are also disturbed by the disease, resulting in a distorted carbohydrate metabolism along with disrupted phytohormone balance and poor tree health and productivity in general (Nehela and Killiny, 2020b). Detection of HLB in its early stages is tough because the disease is asymptomatic and might take years to manifest. More recent developments of detection methods including molecular and spectroscopic methods are being pursued but are currently limited in practice by cost and complexity (Arredondo Valdés *et al*., 2016; Hawkins *et al*., 2010). Even with all the research that has been done, there is still no official cure of HLB. Management strategies can include the combination of the following activities: removal of infected trees, managing populations of *D. citri* using insecticides, and utilizing disease-free planting materials (Li *et al*., 2020). Sustainable solutions are being explored using innovative strategies, including genetic engineering, nanotechnology, and targeted nutrient management (Mubeen *et al*., 2024; Zhao *et al*., 2025).

Broad-spectrum insecticides can be effective in suppressing *D. citri* vector, but there is a concern regarding environmental effects and sustainability. The cost of HLB, control is high and can have an impact not only on the profitability but also on the sustainability of citrus production (Li *et al*., 2020). The nature and interconnectedness of factors that cause HLB, impact necessitate all-inclusive management approaches. The measures aimed at reducing the disastrous impacts of this disease on the citrus industry should include the use of state-of-the-art detection techniques, novel control interventions, and knowledge of the biology and interactions of the pathogen with hosts (Canales *et al*., 2016; Liu *et al*., 2024). To understand and manage the devastating disease HLB, it is important to study it with the perspective of both the pathogen and the citrus host. The phloem-restrictive bacterium, CLas, is what has made HLB, such a tricky mystery to solve; explaining the interactions and effects within the citrus host. The pathogen approach addresses CLas, its modes of propagation, and interactions with plant and insect vectors, including the *D. citri*. This angle can aid in understanding the lifecycle of the pathogen such as movement, gene expression, and participation in symptom manifestation (Pandey *et al*., 2022). The study of genetic and molecular processes of the pathogen may reveal how it can be blocked to prevent its proliferation and virulence in citrus plants (Killiny, 2022). In the host perspective, it is important to study how citrus plants respond to Clas, infection. Knowledge of the molecular and biochemical adaptations in the host may be used to understand how the disease alters host metabolism and derails homeostasis. This information is critical to the detection of plant genes related to resistance or infection vulnerability (Arce-Leal *et al*., 2020; Nehela and Killiny, 2020b). It is also useful to develop genetic modifications to make plants resistant to HLB (B. Hu *et al*., 2021). HLB needs management strategies that deal with the pathogen and the host. The understanding of the pathogen can be used to design antimicrobial agents or genetic engineering to inhibit the pathogen growth. At the same time, the knowledge of host defense allows developing transgenic strains more resistant (D. Ghosh *et al*., 2022; S. Zhang *et al*., 2024). A combination of these plans can result in sustainable management of the citrus industry (Wang and Trivedi, 2013). The HLB research should also take into account the triad of vector-pathogen-host. The interaction between CLas and its psyllid host influences disease spread, which largely impacts the epidemic processes. The knowledge about these interactions can enhance the use of vector control to eventual curb the disease spread (Killiny, 2022; Yan *et al*., 2013). Dual perspective enables the researcher to understand how the pathogen and the host interact and contribute to the biology of each other. An example is how the pathogen has adjusted its metabolic pathways in order to survive, and how the immune response of the host has done the same in order to protect itself. Both understandings are important in developing a comprehensive understanding of the interaction between pathogens and hosts and in creating a wide range of control interventions (B. Hu *et al*., 2021; Nehela and Killiny, 2020b). Comprehensive methodology combining pathogen and host thinking is needed in fighting HLB, the strategy can inform the establishment of novel management practices to improve the resilience and sustainability of citrus production around the world (Wang and Trivedi, 2013).

2. Pathogen Perspective

The latest studies have made a major contribution to the knowledge of genomics of CLas, which causes HLB. The threat caused by this pathogen is significant because it is linked to serious citrus diseases on a global scale (Pandey *et al*., 2022). Identification and characterization of CLas, and *Candidatus Liberibacter* africanus are some of the identified Clas, strains. These strains have been identified using genome analysis that incorporates sequencing of the 16S rDNA among other genetic markers (Garnier *et al*., 2000). Interestingly, a strain of the Cape chestnut tree in South Africa was named as a sub species, *Ca. L. africanus* subsp. capensis, which shows that this pathogen is genetically diverse, given in (Table-1) (Garnier *et al*., 2000).

Table 1: Key Characteristics of HLB

Species/Subspecies	Geographic Distribution	Key Genomic Features	Transmission Vector	Reference
***Candidatus Liberibacter asiaticus* (CLas)**	Global (, Asia, Americas)	Effector proteins (, Las5315mp, SDE115) target host cell functions, suppress immunity	Asian citrus psyllid (*Diaphorina citri*)	Pandey *et al*., 2022; Pitino *et al*., 2016; Du *et al*., 2022
Candidatus Liberibacter africanus	Africa	Identified via 16S rDNA sequencing	African citrus psyllid (*Trioza erytreae*)	Garnier *et al*., 2000
Candidatus Liberibacter africanus* subsp. *capensis	South Africa (Cape chestnut)	Genetically diverse subspecies		Garnier *et al*., 2000

The complete genome of Clas, has played a key role in the study of its functional genomics and the interactions of biomolecular events of this pathogen with citrus plants. These are the identification of effector proteins capable of controlling the functions of host cells to facilitate infection (Pitino *et al*., 2016). As an example, Las5315mp has been shown to localize in the chloroplasts and cause cell death and callose deposition in the host plants (Pitino *et al*., 2016). Studies have also given information on the influence of Clas, on the physiological processes of plants. Metabolomics studies of infected plants have demonstrated alterations including an increase in the content of sucrose in the affected leaves which can be attributed to the impact of the pathogen on plant metabolism (Freitas *et al*., 2015). Moreover, genomic research has revealed host genes which can play a role in resistance or susceptibility to the pathogen (B. Hu *et al*., 2021).

D. citri is a major carrier of this pathogen. The study of the relationship between Clas, and this carrier has illuminated the mechanism of pathogen transmission and adaptation in the insect host which is paramount to controlling the spread of HLB (Grafton-Cardwell *et al*., 2013). Such developments in the field of genomics do not just increase the amount of information on how Clas, cause HLB but also offer possible avenues of devising ways through which this citrus disease can be more efficiently controlled (Zhao et., 2015). Although the complete control approaches are yet to be designed, the current aim is to learn more about the interactions between plants and pathogens and the potential availability of the resistance genes that may become crucial in the future control and management approaches (J. Du *et al*., 2023). The effectors and virulence factors of Clas, are important in the pathogenesis of HLB, a fatal infection of citrus plants. These considerations and influences play a role in the interaction of the pathogen with the host and cause infection and development of symptoms in several ways (Ying et al., 2019).

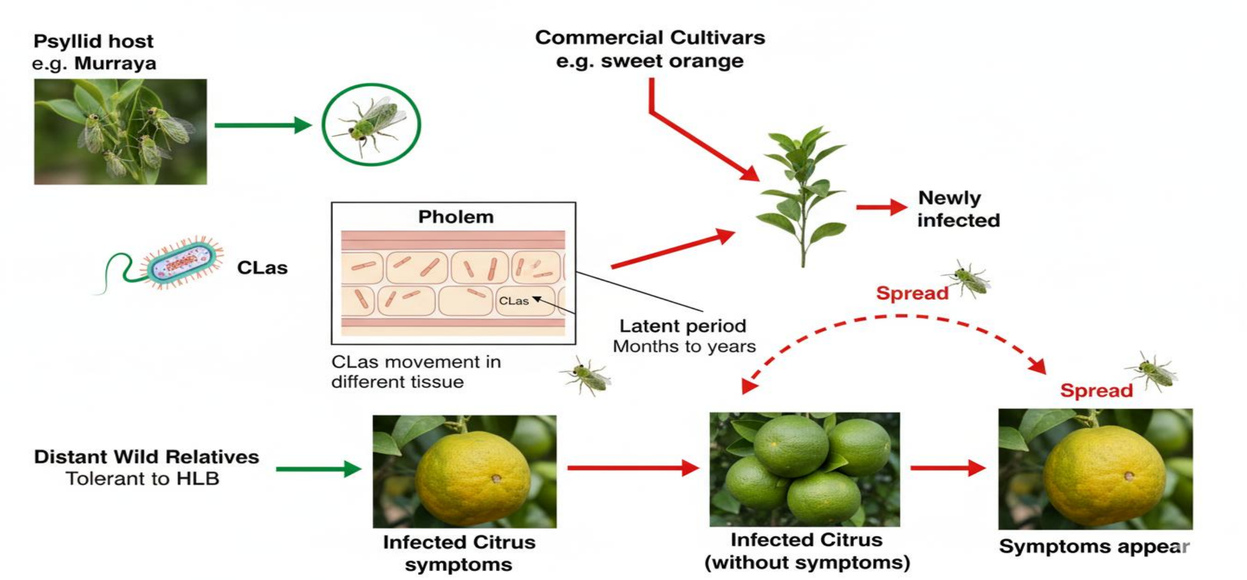
CaLasSDE115 is an effector gene of Clas, that has been shown to be an important contributor to early colonization of citrus plants. Its overexpression upregulates Clas, growth and symptom maturation. This effector alters the transcriptional regulation of the genes that are linked to systemic acquired resistance (SAR) response, aggravating the symptoms of HLB, in citrus plants (M. Du *et al*., 2022). The virulence factors inducing defensive responses have been observed in heterologous expression in the *Nicotiana benthamiana,* including CLIBASIA-05150, which localizes the Golgi apparatus and triggers the cell death and growth inhibition. These are protein-level factors, which may indicate their involvement in the regulation of host cellular functions to undermine plant defense mechanisms, thereby playing a role in the development of HLB symptoms (Ying *et al*., 2019). Targeting Senescence and Host Susceptibility the SDE1-delivered effector Senescence-regulator, suppresses defense-related proteins and triggers senescence, which is similar to the symptoms of Clas, infection including yellowing of leaves and accelerated senescence. When this effector is expressed in model plants, it leads to premature aging that subsequently makes the plants more vulnerable to CLas (Clark *et al*., 2020). CLas-secreted polypeptides, such as SECP8, are broad-spectrum immunosuppressive. They suppress numerous immune responses, including in response to other pathogens, and increase the susceptibility and the severity of symptoms in infected citrus plants. SECP8 in particular suppresses immunity-related gene, favoring HLB, symptoms (Shen *et al*., 2022). A second effector, a prophage-encoded peroxidase, is released during infection and suppresses the host oxidative stress responses, which is essential to the pathogen survival and enables the disease to remain silent over prolonged periods. Such an effector inhibits the action of reactive oxygen species-mediated defense signaling pathways that play a central role in early plant defense mechanisms (Jain *et al.*, 2015). Recent discoveries on HLB, underscore a number of very important factors associated with colonization of the pathogen, phloem transport, and spread by vector. HLB, is a disease caused by the phloem-restricted bacterium Clas, and has a major impact on citrus production worldwide. The phloem is colonized by the disease pathogen, which reduces the yield and causes death of trees because of disrupted nutrient flow. The *D. citri*, is the main carrier of the disease and a host to Clas, as shown in (Figure-2) (Pagliaccia *et al.*, 2017; Killiny, 2022).

Recent studies have been directed on the determination of the intricate associations between the bacteria and *D. citri,* host. Mutualistic properties emphasize the nature of the relationship between the vector and the pathogen in which the pathogen, regardless of its adverse impacts on the *D. citri,* including the development of abnormal feeding behavior and high fecundity, facilitated its transmission by promoting the fitness of the vector (Killiny, 2022). Developments in molecular and biochemical studies have defined the routes of acquisition and transmission of Clas, by *D. citri*, providing information about possible intervention sites (Killiny, 2022). Regarding the transmission, HLB is fast spreading because it is asymptomatic and it is not distributed evenly in infected trees, which makes it difficult to detect and control in the early stages of disease development (Gottwald, 2010). Most methods of controlling this pathogen are usually aimed at several goals: inhibition of bacterial proteins, antimicrobial compounds, biological control of the *D. citri*, vector (D. Ghosh *et al.*, 2022). The application of chemical treatments, including penicillin G potassium, and biological treatments as a part of integrated management strategies also highlights the need to use sustainable solutions to control the number of *D. citri* (M. Zhang *et al.*, 2019). As of recent, serological assays have been used to detect Clas, through the release of distinct proteins by the pathogen. They serve as proteins biomarkers, making it easier to detect infected trees earlier and more precisely, which is beneficial in managing this disease (Pagliaccia *et al.*, 2017). These initiatives emphasize the multisided methodology needed to control the risks introduced by HLB, with the main emphasis on early detection, control of vectors, and integrated control measures to reduce the effects of this disease in citrus industries all over the globe (Da Graça & Korsten, 2004; J. H. Graham *et al.*, 2024).

Innovative molecular diagnostics and omics-based technology have recently aided in greatly enhancing the detection of HLB, pathogen, especially CLas. The developments are important since HLB, is a significant threat to citrus industries across the world. Several molecular diagnostics and omics methods have been used to improve the discovery of HLB, pathogen (Vandaveer., 2004). A significant improvement is the application of a recombinase polymerase-based isothermal amplification coupled with a subsequent lateral flow assay (HLB-RPA-LFA). The technique is designed to work with the fast detection of Clas, and is a sensitive cost-efficient, and accessible alternative to established polymerase chain reaction (PCR) techniques (D. K. Ghosh *et al*., 2018). The method specifically applies to the identification of the pathogen in the field, which is why it is available to farmers, surveyors, and quarantine programs. There have also been longitudinal transcriptomic, proteomic and metabolomic studies of citrus orchard response to infection (Suh., et al 2021).

Such investigations have shown pronounced variations in transcripts, proteins, and metabolites in citrus trees as soon as two weeks after being inoculated with Clas, and indicated potential to detect the disease early and before the onset of symptoms (Ramsey *et al*., 2020). Such a combined method of monitoring molecular changes in the plant could help to have diagnostic technologies developed. Further, the limit of detection of techniques such as TaqMan real-time PCR has been demonstrated to be ten to hundred times larger than standard PCR, which facilitates the successful identification of Clas, prior to manifestation of symptoms (W. Li *et al*., 2007). The sensitivity of this method is high and enables intervention and better management of the spread of HLB, at an early stage. Another promising line of early detection has been the innovations in volatile organic compound (VOCs), analysis. The differential mobility spectrometry and gas chromatography methods used to determine VOCs produced by infected trees have been found to be very accurate even prior to the appearance of symptoms. The method has a quick, low-cost, and field-deployable mechanism of diagnostics to supplement those DNA-based (Aksenov *et al*., 2014). Finally, it has been developed serological assays that use a Clas, secreted protein as a biomarker. These assays utilize a polyclonal antibody to measure the concentration of the secreted protein, and they are a high-throughput and cost-effective complement to the available quantitative PCR techniques (Pagliaccia *et al*., 2017).

Figure 2: Dissemination of CLas



3. Citrus Host Perspective

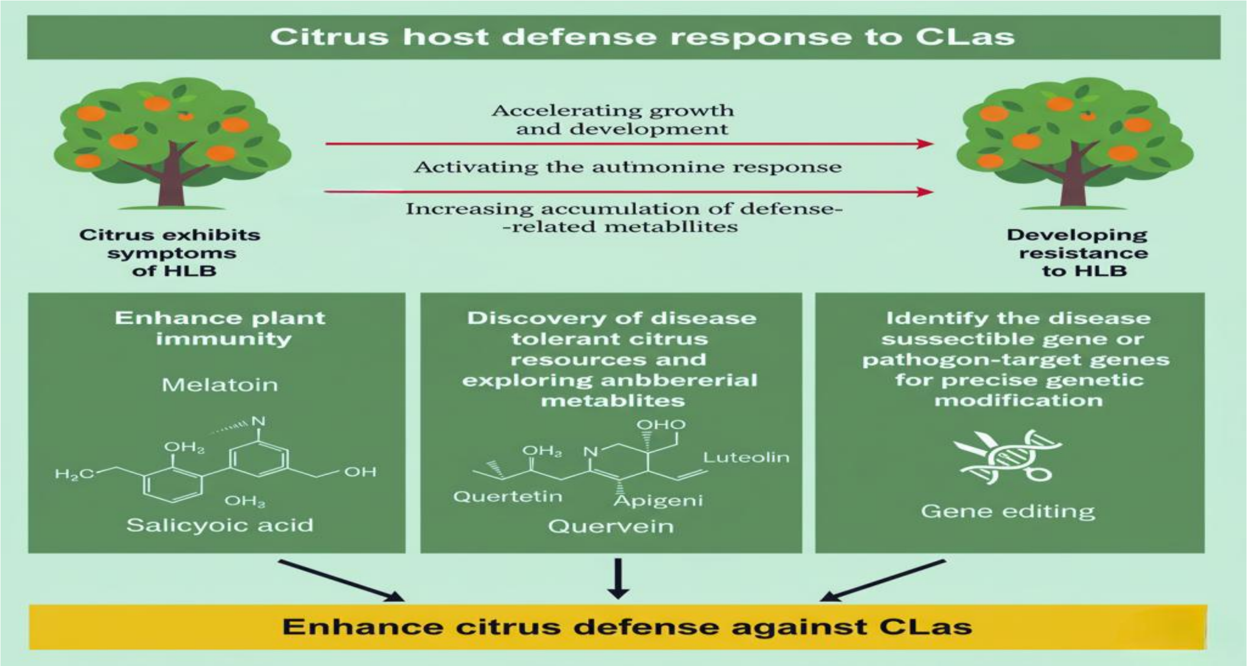
Complex molecular mechanisms involving multiple signaling pathways, defense responses and interactions between citrus plants and the bacterium Clas, are the main way of the citrus plant to perceive and signal HLB, infection. Effector Proteins and autophagy Clas, uses effector proteins to regulate host cellular processes. One effector, SDE4405, interacts with autophagy-related proteins (ATG8s), to allow bacteria to grow by inhibiting host immune systems. It is a negative regulation of plant defense, promoting autophagic processes that are beneficial to the pathogen through this interaction (Shi *et al*., 2023). Defense-related proteins in lemon plants, such as Las infection, are decreased and some elemental concentrations increase (e.g. Zn). This indicates that there is a selective build-up of proteins and components that might reflect a general response mechanism of citrus plants to the Las infection (Nwugo *et al*., 2013).

Methyl Salicylate (MeSA), Signaling Some tolerant citrus types such as sour pomelo have been associated with a high concentration of MeSA, a major signal of salicylic acid (SA) pathway activation, and HLB, tolerance. The pathway is important in activating the SAR, in plants that help them protect against Las, as given in (Figure-1) (Zou *et al*., 2019).

Arabidopsis thaliana NPR1, overexpression in citrus increases resistance to HLB, by increasing transcription of pathogen-associated molecular patterns, as well as signaling pathway genes. NPR1, collaborates with certain proteins to elevate innate immunity to defend citrus against HLB (Qiu *et al*., 2020).

In vulnerable citrus species, both second messengers of energy metabolism and defense-related gene expression change dramatically in the immediate post-infection period. Transcriptomic analyses show that gene changes affect hormone biosynthesis, metabolism, and photosynthetic pathways, and the plant is trying to regulate energy and stress during infection (Wei *et al*., 2021). Infection is associated with major biochemical alterations including elevation of adenosine triphosphate (ATP), and hydrogen peroxide (H2O2), in infected tissues that are correlated with the severity of HLB symptoms. This means that it is a stress reaction and that these molecules play a role in signaling and resistance to pathogens (Pitino *et al*., 2017). HLB infection results in the buildup of starch in the leaves of diseased citrus plants. This is associated with the up-regulation of genes involved in the synthesis of starch, such as adenosine diphosphate (ADP), glucose pyro phosphorylase and starch synthase resulting in excessive production of starch. The disease also affects the phloem transport system, which normally carries the carbohydrates leading to starch accumulation in the leaves (Kim *et al*., 2009).

Figure 1: Citrus Host Defence Response to CLas



This infection by Clas, causes the deposition of callose, a carbohydrate polymer which blocks sieve pores in the phloem. This process is aided by the up-regulation of genes involved in the biosynthesis of callose as a defense response in a plant in an attempt to prevent the proliferation of the pathogen. Nevertheless, when the callose deposition is too high, it causes a blockage of the phloem and the formation of nutrient and water transport systems in the plant (Kim *et al*., 2009; Ma *et al*., 2022). Source-sink disruption HLB, causes serious disturbance of the source-sink relationships of the plant. It is further disturbed by the impact of the disease on the photosynthetic efficiency and carbohydrate partitioning of the plant. The extreme starch storage shows that there is a sink constraint, i.e., the usual translocation of sugars between the source (leaves) and sink (fruits, roots) is disrupted. This causes low development of fruit and low yield (Kim *et al*., 2009; Suh, Vincent, *et al*., 2021).

The phloem-related dysfunctions related to HLB, such as accumulation of starch, deposition of callose, and disruption of the source-sink, profoundly affect the physiological activity of citrus plants causing a decrease in growth and fruit production. These malfunctions are mainly initiated by the loss of gene expression related to the defense mechanisms, carbohydrate metabolism, and phloem transport systems of the plant (Kim *et al*., 2009; Ma *et al*., 2022; Suh, Vincent, *et al*., 2021). The response of the host to HLB, the crippling citrus disease caused by the bacteria Clas, is heavily influenced by defense reactions and stress physiology. different plant metabolites and stress-related compounds are important in this interaction (Shen et al., 2022). Among the important components are reactive oxygen species (ROS), and antioxidants. Oxidative stress is commonly caused by the manipulation of host plant metabolism by HLB, and its vector as evidenced by the elevation of ROS levels. This in itself requires a vigorous antioxidant reaction in the plant to counteract oxidative damage (Rawat et al., 2917) An example of such phytohormonal approach is the incorporation of melatonin in plant responses to enhance antioxidant defenses. Not only does melatonin increase antioxidant functions, but also regulates the concentration of various phytohormones such as, salicylates and auxins, which helps to defend and may lower the percentages of bacteria inside the infected plant (Nehela and Killiny, 2020a). Moreover, volatile terpenoid biosynthesis, such as, that of 2-caryophyllene and 2-ocimene, is greatly stimulated during HLB, infections and also in tolerant citrus varieties, such as the pomelo; in this case, the 'Shatian'. They belong to the plant-wide defense against various stressors both as direct-acting deterrents to pathogen and as defense-pathway signaling molecules (Wen *et al.*, 2023).

The importance in relation to HLB, are nutrient imbalances, especially those that involve the phloem functionality. The disease affects carbohydrate metabolism and hormone signaling pathways and change the overall defense capabilities of the plant (Rao et al.,2018) The energy metabolism and the hormone biosynthesis pathways, including those of auxins and cytokinin's, are up-regulated in tolerant cultivars. These hormones play a significant role in growth and phloem regeneration, hence offering a partial tolerance mechanism to keep the plant functions active despite infection (Suh, Zhang, *et al.*, 2021). Genetically, it is important to note that the expression of stress-related genes, including secretory protein of the cysteine-rich, or CAP, family are important in the regulation of stress responses. These genes are also important in response to biotic and abiotic stresses, which illustrates the complexity of genetic and metabolic response mechanisms in the plant in response to HLB (Mahmoud *et al.*, 2024).

Also, the pathogen can occasionally compromise host defense mechanisms by manipulation of autophagic processes. The pathogen-secreted effector is called (SDE4405), and can promote autophagy, which has the ability to suppress innate immune responses of the plant, which represents an advanced strategy used by the pathogen to promote its growth and disease development (Shi *et al*., 2023). RS and stress physiology factors including ROS, antioxidants and nutrient management are interrelated with metabolic and genetic adaptations, and play a vital role in influencing citrus host response to HLB. This knowledge is critical towards the designing of specific programs to control this multi-faceted disease (Da Graça *et al*., 2015; Suh, Zhang, *et al*., 2021). Specific characteristics of tolerant citrus rootstocks along with allied species are attributed to their resistance to HLB, a destructive disease of citrus plants. Some of the important characteristics and processes that confer tolerance have been found (

HLB-tolerant cultivars exhibit sustained phloem regeneration and plant growth, which play a vital role in preserving the health and functionality of the vascular system impaired by HLB (Suh, Zhang, *et al*., 2021). HLB, tolerance is associated with certain metabolic pathways. The metabolism of aspartate and glutamate, purines, and some plant hormone biosynthetic pathways such as auxins and cytokinin's involved in plant growth and phloem regeneration are upregulated in tolerant varieties. On the other hand, metabolites commonly associated with plant defense reactions linked to SA are suppressed in tolerant cultivars (Suh, Zhang, *et al*., 2021).

Tolerant citrus varieties are also more likely to have an elevated concentration of amino acids or phenylalanine, tyrosine, tryptophan, lysine and asparagine that are involved in plant defense. They also have high flavonoid, terpenes, and volatile compounds which possess antimicrobial properties, and may limit the movement and growth of pathogens (Killiny & Hijaz, 2016; Rao *et al*., 2018).

Experiments in resistant *Poncirus trifoliata* and hybrids have shown that some constitutive disease resistance (CDR), genes are more highly expressed, and receptor-based pathways leading to the expression of defense mechanisms are increased. It involves the repression of the production of gibberellin and the induction of cell wall fortification and (WRKY), transcription factors which are considered as tolerance contributors (Curtolo *et al*., 2020; Rawat *et al*., 2017). Some citrus relatives e.g. *Eremocitrus glauca* and Micro-citrus species are completely resistant to the HLB, pathogen and may be used in breeding to provide HLB, resistance genes. These species can be used with citrus and have potential as new rootstocks or inter-stocks (Alves *et al*., 2021; Ramadugu *et al*., 2016).

4. Integrated Insights

Recent research has contributed greatly to the current knowledge of the interaction between the pathogen effectors and citrus host signaling pathways in HLB, a deadly disease of the bacterium CLas. Among the important facts is that the bacterium is capable of suppressing plant defenses by degrading SA, which is one of the main plant immunity components. The bacterium also expresses a functional salicylate hydroxylase (SahA), which breaks down SA, thus making citrus plants more susceptible to nonpathogenic and pathogenic infections by weakening their defense against them (J. Li *et al*., 2017). Additionally, it has also been shown that citrus metabolites play a role in the development of HLB symptoms. The effects of these metabolites on the disease include homeostasis of carbohydrates, phytohormones and antioxidants. It is important to learn how these metabolic pathways are altered by Clas, in order to develop effective measures to control HLB (Nehela and Killiny, 2020b). Also, Salicylic Acid Carboxyl Methyltransferase (SAMT1), is reported to induce HLB tolerance in citrus by modulating SA homeostasis, which plays a central role in plant defenses (Zou *et al*., 2021).

The other significant development is in the detection strategies of HLB. Those that study it have devised ways and means of identifying pathogen-secreted proteins in citrus used as a biomarker to diagnose HLB even without the presence of symptoms. The method improves the ability to detect diseases at an early stage, hence making the disease easier to control (Pagliaccia *et al*., 2017). Moreover, HLB transmission models indicate the significance of the *D. citri* vector, as well as show that vectors play a decisive role in initial infection but not in subsequent within-tree transmission. According to this model, internal movement between the flushes is also involved in the development of the disease (Chiyaka *et al*., 2012). Recent developments in dual RNA-seq and systems biology have helped us to greatly improve on our knowledge about the interactions between pathogens and hosts especially in the plant system with citrus hosting pathogens. Dual RNA-seq enables the expression department of both parties and the pathogen to be analyzed at the same time giving every detail of the molecular interaction (Pandey 2022). The dual RNA-seq represents the outstanding ability to explain both the host and the pathogen gene expression patterns in infection and to identify the important information regarding the pathogen load and development of symptoms in the host. It has been used on many different pathogens and hosts, and a growing literature is highlighting the capability of this method to reproduce the complexity of host-microbe interactions *in-vivo* (Naidoo *et al*., 2017). More recent work has used dual RNA-seq to investigate interactions between pathogens and vulnerable or resistant host variants, e.g. between *Fusarium circinatum*, and pine species. Among these findings have been important differences in the expression of pathogen genes (including, but not limited to, reduced expression of ergosterol biosynthesis genes in resistant hosts) and the implication that key phytohormone signaling pathways mediate host resistance and susceptibility (Visser *et al*., 2019).

In addition, dual RNA-seq has been used to simulate the interaction dynamics over time, which provides information on how pathogen virulence factors and host immune responses are regulated over time. As an example, one study on *Pseudomonas plecoglossicida*, and its host has been done, which has identified dynamic changes in gene expression in order to point to the motility and flagellum assembly of the pathogen in the peak of infection and the up-regulation of immune-related pathways in the host (Tang *et al*., 2020). Other omics technologies, including proteomics and metabolomics, and systems biology, also contribute to the information provided by dual RNA-seq by offering a multi-dimensional perspective of host-pathogen interactions. This has enabled scientists to discover major regulatory networks and pathways that regulate the development of ailments and the success of the host immune reaction (Naidoo *et al*., 2017). In general, the convergence of dual RNA-seq and systems biology still reveals the highly complex interaction of pathogen load and host symptom evolution, which will allow creating more effective disease management methods and disease-resistant crop lines. The results are encouraging, but additional implementations of these cutting-edge methods may shed more light on citrus host-pathogen interactions (Naidoo *et al*., 2017; Visser *et al*., 2019).

5. Management & Breeding

Recent developments in the control of vector and sanitation of orchards have played a critical role in the control of the devastating disease HLB, in the citrus industry. The *D. citri*, which transmits the HLB pathogen CLas, is the main target of vector control. The major advancement has been the adoption of area-wide management plans, such as in Texas and California, where management has been more effective in reducing the propagation of the disease than Florida. These are the intensive use of systemic insecticides and foliar sprays to manage the populations of *D. citri* (J. Graham *et al*., 2020: and Moreira *et al*., 2019). Considerations of economics are quite influential in these strategies. Evidence in Florida has demonstrated that although insecticidal management in combination with supplemented foliar nutrition can sustain an increased yield, it is not always economically viable because of the high cost of treatment (Stansly *et al*., 2013). The use of the frequency and timing of insecticides to achieve cost-effectiveness in disease control has recently been studied (Monzo and Stansly, 2017).

Improving tree density (through cultural practices) has also demonstrated potential in the treatment of HLB. According to a study conducted in Brazil, in particular in the State of Sao Paulo, an increase in the density of trees has the potential to reduce the incidence of HLB, by reducing the ratio of infected trees, and increase the overall profitability of affected areas (Moreira *et al*., 2019). Moreover, regional management programs have been effective in Brazil, both by using preventive control and coordinated *D. citri*, management on large scales, as well as by making citrus industry activities in the country remain viable (Bassanezi *et al*., 2020). In addition, a regionalization based on risk has been suggested to control HLB vector in places that have not been infested by the disease, including the Mediterranean Basin. This is through organized pest control throughout specific regions to reduce the introduction and transmission of vector and provide a conceptual model in case of future outbreaks (Galvañ *et al*., 2023).

Although great progress has been made, it is important that current research and management methods are adapted because of the multidimensional nature of HLB, and its vector. Improvements in managing vectors, economic evaluations, and cultural management actions are all developing and serve as a base to design more sustainable and effective management strategies One of the strategies that are being used to address HLB, resistance in Citrus crops is breeding, rootstock selection, and CRISPR-based genome editing (J. H. Graham *et al*., 2024). Historic breeding approaches are highly constrained, especially when working with citrus, by aspects like polyploidy and sluggish juvenile phases. Recent tasks have been directed at HLB, resistance identification in other species of citrus. The long-term field experiment tested sixty-five citrus accessions along with thirty-three others of related genera in natural diseases and found two immune, six resistant and fourteen tolerant accessions. Certain relatives of citrus used in Australian (*Eremocitrus* and *Microcitrus*) were found to be resistant and could be useful in breeding programs where HLB resistance needs to be improved in cultivated citrus (Ramadugu *et al*., 2016). Rootstock selection plays an important role in enhancing citrus resistance to HLB. USDA Super Sour breeding strategy represents a new direction of citrus rootstock breeding. This strategy has demonstrated potential by increasing the range of germplasm, shortening the interval between cross and cultivar commercialization, and by increasing the number of new hybrids under consideration. More than three hundred fifty new hybrid rootstocks have been tested, and many have been found to be better yielding and generally healthier in HLB-infested areas, than traditional rootstocks (Bowman *et al*., 2021). Secondly, field trials monitored field tolerance in some scion/rootstock combinations under high HLB, pressure to find other combinations that remain growing and fruiting despite infection (Stover *et al*., 2016).

CRISPR/Cas9 system provides a fast and accurate approach to the insertion of disease resistance genes. Crispr-based citrus alteration is being employed in the production of disease resistant citrus. Targeted genome editing, including the modification of susceptibility genes (e.g., CsLOB1), has demonstrated compelling outcomes in minimizing disease symptoms including citrus canker, and such approaches are being expanded to treat HLB (Jia *et al*., 2017). Improved CRISPR technologies are opening the door to the creation of citrus varieties strong against various pathogens (Sun *et al*., 2019). HLB, is a severe threat to world citrus production. More recent developments have investigated a range of approaches to controlling this disease, such as RNA interference (RNAi), antimicrobial peptides (AMPs), and microbiome engineering, as shown in (Table- 2) (Zhang et al., 2024). RNAi is an emerging technology in the control of HLB, especially in the control of the disease transmitting vegetable, the *D. citri*, that carries the disease-causing bacterium CLas (Hajeri *et al*., 2014). An RNAi-mediated *Citrus tristeza virus* (CTV)-based approach has been designed to induce genetic silencing in the *D. citri*, with the objective of disabling its capacity to transmit the pathogen by targeting certain genes involved in the development of nymphs. The strategy restricts the transmission of Clas, and has potential to act as a control measure (Hajeri *et al*., 2014). AMPs are now a possible antimicrobial agent against HLB. These compounds are highly effective and have low levels of toxicity when compared to traditional antibiotics, providing a lasting solution to the disease. Nevertheless, additional analysis is required to determine their business feasibility (X. Li *et al*., 2021). The design and evaluation of novel compounds and a better comprehension of the processes through which they act is a key to their implementation in controlling HLB (Munir *et al*., 2017).

Microbiome engineering is the use of the beneficial communities of microbes in citrus plants to enhance the resistance to HLB. The objective of this method is to control the native microbiota of the plant to prevent pathogen colonization and increase host resistance. Recent developments have found certain antimicrobial metabolites inherent to HLB-tolerant varieties, and it is possible that engineering these pathways will result in the creation of more robust citrus species (Rao *et al*., 2018). The ongoing research on the topic aims at developing an engineering approach to enhance the defense of plants through the engineering of metabolic pathways (Rao *et al*., 2018). Host perspective Nutritional and cultural therapies complement molecular means to control HLB. Since HLB, is a complex and multifaceted disease, integrating the use of these therapies with molecular interventions can help to improve overall management and control of the disease (Yan et al., 2013). Nutritional control, especially the steady and constant use of macro- and micronutrients, may reduce stress in trees with HLB. It has been shown that an increase in nutrient supply can lead to improvements in root health, canopy size, and tissue nutrient concentration, which yields a favorable environment in which tree health and productivity can be supported (Kadyampakeni and Chinyukwi, 2021). There have also been biologically enriched nutritional programs (bENPs). Such programs have the potential to decrease pathogen load in phloem tissues, yield higher fruit, and regulate the expression of host genes, which makes them a viable, sustainable, and cost-effective approach to the management of HLB (Makam *et al*., 2023).

High density planting, irrigation and proper nutrition have been found to alleviate the effects of HLB, on orchard production and survival. They are used to stabilize the profitability and competitiveness of citrus orchards in citrus-infested regions in HLB (Bassanezi *et al*., 2020). The disease can be slowed down by using preventative cultural methods, including clearance of diseased trees and elimination of vector, although they should be combined with the molecular approach that will directly address the pathogen (Moreira *et al*., 2019). Molecular strategies, such as genetic engineering and application of antimicrobial peptides and nanoparticles, have potential to be used directly against the HLB, pathogen. Nonetheless, the combination of nutritional and cultural interventions may offer a further dimension of resilience to enhance the overall health of the citrus trees and their ability to withstand stress (X. Li *et al*., 2021; Mubeen *et al*., 2024).

Table 2: Management Strategies for HLB

Strategy	Description	Effectiveness	Challenges	Reference

Vector Control (Insecticides)	Systemic insecticides and foliar sprays to control Asian citrus psyllid	Reduces psyllid populations, slows HLB spread	Environmental concerns, high costs	Graham *et al.*, 2020; Stansly *et al.*, 2013
Nutritional Therapies	Enhanced macro- and micronutrient supply to reduce tree stress	Improves root health, yield	Not a cure, variable efficacy	Kadyampakeni & Chinyukwi, 2021; Makam *et al.*, 2023
Cultural Practices	High-density planting, tree removal, irrigation optimization	Reduces HLB incidence, improves profitability	Labor-intensive, region-specific	Bassanezi *et al.*, 2020; Moreira *et al.*, 2019
RNAi-Based Control	Silencing psyllid genes to reduce CLas transmission	Targets vector transmission	Requires field validation	Hajeri *et al.*, 2014
CRISPR Genome Editing	Editing susceptibility genes (CsLOB1) to enhance resistance	Promising for developing resistant varieties	Regulatory hurdles, long development time	Jia *et al.*, 2017; Sun *et al.*, 2019

6. Challenges and Future Directions

Critical knowledge gaps in culturing and functional genetics of HLB, pathogen especially CLas, that impede the progress in understanding and managing this disease are associated mostly with the fastidiousness and complexity of the interactions between the pathogen and the host plant

(Wang et al., 2013). The main problem is that Clas, cannot be cultured *in-vitro*, and therefore this greatly impedes the research of its pathogenic mechanisms and biology. The bacterium is phloem-dwelling and hard to grow in the laboratory, which does not allow a thorough laboratory examination (B. Hu *et al*., 2021).

The CLas-pathogen interaction is highly complex with intricacies that make the pathogenicity and resistance mechanisms difficult to elucidate (B. Hu *et al*., 2021). Availability and use of functional genomic tools to clarify the genes implicated in Clas, pathogenicity as well as identify genetic pathways imparting resistance against citrus plants have gaps. This restricts the capacity to alter these genes to create a resistant variant of citrus (Qiu *et al*., 2020). Interaction between plant metabolism and phenotype CLas-infected microbiome is not completely comprehended. More of these studies should be conducted with integrative methods such as multiomics analysis and machine learning to better understand these dynamics and identify possible solutions (J. Li *et al*., 2023). The genome of the CLas-carrying *D. citri*, is complex and is thus difficult to sequence and annotate, making it difficult to develop genetic-level control strategies against this organism (Saha *et al*., 2017). Commercial citrus cultivars do not have much resistance to HLB. Genetic engineering of disease resistance, e.g., expressing modified thionins, has had some promise and is not a widespread solution yet (Hao *et al*., 2016). According to recent innovations in early detection of HLB, a number of possible solutions can be offered to the problem of the control of this severe plant disease. One of these developments is the establishment of multiplex molecular detection methods that can add specificity and sensitivity to pathogen detection. The introduction of a variety of different innovations, e.g. multiplex PCR, polyvalent PCR, or non-isotopic molecular hybridization, led to reduced time and cost of diagnosis by detecting multiple plant pathogens simultaneously (Pallás *et al*., 2018). Further, progress in nanotechnology and microfabrication technology has enhanced the technique of viral detection which can be applied to plant pathogens such as those causing HLB. These technologies improve the detection limits, operational simplicity and cost-effectiveness of diagnostics and make them more feasible to be used widely (Cheng *et al*., 2008). Additionally, the combination of microchip capillary electrophoresis and electrochemical detection systems provides the opportunity of highly miniaturized, rapid and efficient assays. They can be optimal on-site and rapid HLB, detection systems because of their portability and less demanding laboratory infrastructure (Vandaveer *et al*., 2004).

The integration of machine learning models and superior data processing capabilities into detection systems increases selectivity and efficiency of pathogen identification by analyzing nucleic acids as species-specific biomarkers of HLB (Feazel *et al*., 2011). To attain sustainable management of HLB, field validation of the molecular solutions is essential due to a number of reasons. HLB is a disease caused by CLas spp., a bacterium that inflicts severe effects on citrus crop production and has no cure (Hall *et al*., 2012; J. Li *et al*., 2019). Recent developments have emphasized several novel approaches, such as, molecular and biochemical assays, used to diagnose and treat HLB. These techniques examine how the pathogen enters the host plant and its effects on the host, which is critical in the establishment of sustainable management practices (Mubeen *et al*., 2024). An example of such is nanotechnology, antibiotics, and genetic engineering technologies which have the potential to create combined HLB, management methods (Mubeen *et al*., 2024).

In addition, the molecular approach to understand the interactions between plant metabolites and plant-associated bacteria can be used to determine the key pathways and possible solutions to control HLB, by regulating bacteria in citrus plants (J. Li *et al*., 2023). Machine learning systems combined with multiple forms of omics data also predicted metabolic pathways that might influence microbial community compositions, which might be used to develop HLB-tolerant citrus species (J. Li *et al*., 2023). Field validation makes sure that those molecular solutions work under real growing conditions to deal with variability and complexity of the HLB, pathosystem in new environments. It aids in how best treatment regimens can be given, how better disease can be identified, and how the long-term effects of molecular interventions on citrus health and yield can be evaluated. It is essential to transfer the success of the experiment to a large-scale, sustainable implementation of HLB, in various citrus-growing areas (Blaustein *et al*., 2018; S. Li *et al*., 2020). Multi-omics breeding pipelines are fast becoming known to expedite the breeding process of HLB-tolerant citrus varieties. With the combination of multiple omics technologies e.g. genomics, transcriptomics, proteomics and metabolomics, researchers have the opportunity to elucidate complex interactions in citrus plants that result in disease tolerance (Suh et al., 2021)

It has been demonstrated that the combination of metabolomics and microbiomics can offer important clues to the relationships between plant metabolism and microbes linked to HLB, tolerance. As an example, some plant pathways, including the ABC transporters and terpene biosynthesis, have been associated with changes in microbial communities, implying the development of approaches to breed HLB-tolerant citrus (J. Li *et al*., 2023: Jan et al., 2025). Comparative transcriptome analysis has revealed that there are naturally tolerant mechanisms in some species or cultivars of citrus. An example of a tolerant crop to HLB, is citrus *hystrix*, which exhibits tolerance due to active carbohydrate metabolism and photosynthesis, as well as upregulated defense-related genes, which can be used in breeding programs (Y. Hu *et al*., 2017).

Proteomic research has shown that heat treatments have the ability to modify the expression of proteins that are linked to HLB, resistance. Detection of differentially expressed proteins, including heat shock proteins, can be used to breed more tolerant animals, with the choice of these genetic traits potentially increasing tolerance (Nwugo *et al*., 2016). High-density genetic mapping and QTL analysis have revealed that there are certain genetic loci that are related to HLB tolerance. These loci offer both molecular breeding and genetic engineering targets and avenues to transfer tolerance phenotypes into commercially useful citrus varieties (Huang *et al*., 2018). There are species which are naturally tolerant to HLB, such as the Australian finger lime. It has been postulated that these species have special qualities, including enhanced phloem regeneration and altered gene expression, which can be exploited through breeding schemes to create tolerant cultivars (Dutt *et al*., 2021; Weber *et al*., 2022). It has been noted that some metabolites like flavonoids and terpenes are much more abundant in HLB-tolerant varieties. These metabolites have the ability to hinder the pathogen and consequently aid in defense mechanisms in the plant. The results open the door to breeding approaches that are metabolite-based (Rao *et al*., 2018)

7. Conclusion

The latest advancements in the pathogen-host interactions in the management of HLB, have played a major role in influencing the new strategies to be adopted to reduce this devastating disease of citrus. The given context does not mention HLB, directly but it addresses the developments in the pathogen-host relationships and pathogen control in other contexts, which can be applied to HLB, management similarly. Understanding the molecular nature of interactions between the pathogen and the host is one of the most powerful tools in the management of plant diseases, including citrus. More recently, multi-omics methods, including transcriptomics, proteomics, and metabolomics, have been exploited to gain a more detailed picture of these interactions. Such technologies facilitate the discovery of the molecular mechanisms of host resistance and pathogen virulence and, therefore, potential disease management biomarkers. Genetic resistance technology using modern genomics has been a turning point in controlling disease in plants. The development of resistant citrus varieties can be dependent on the identification of new host resistance genes and the molecular pathogenesis knowledge that can be key in the development of resistant citrus varieties. These innovations can bring a substantial decrease in the number of chemical controls and more sustainable. Along with genomic and biotechnological methods, an in-depth look of the host-pathogen relationship also helps to detect new chemical and biological control agents. These agents have the advantage of acting at particular stages of the life cycle of the pathogen or the interaction of the pathogen with the host and hence can mitigate disease epidemic and severity without necessarily using broad-spectrum pesticides that may be harmful to the environment.

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