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Comprehensive review of *Acidovorax citrulli*: Insights into pathogenesis, management strategies, and advances in sustainable plant pathogen control

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Abstract
Acidovorax citrulli is a gram-negative bacterium recognized as the causative agent of bacterial fruit blotch (BFB) in cucurbit crops. This review aims to illuminate the mechanisms of genetic variability exhibited by *A. citrulli*, explore its interactions with host plants, and assess the implications of these dynamics for sustainable crop management strategies. Furthermore, the review highlights the pivotal role of innovative tools and technologies, such as whole-genome sequencing and CRISPR gene editing, which are revolutionizing our understanding and management of this pathogen. Ultimately, this work seeks to promote sustainable agricultural practices and enhance food security by bridging fundamental research with practical, real-world applications.

Keywords: *Acidovorax citrulli*, genetic diversity, cucurbits, bacterial fruit blotch, integrated pest management, genomic tools

Introduction

Acidovorax citrulli is a gram-negative bacterium causing bacterial fruit blotch (BFB) in cucurbits, particularly affecting watermelons and melons (Burdman & Walcott, 2012) [8]. The pathogen spreads globally through contaminated seeds, posing a significant threat to the cucurbit industry (Bahar & Burdman, 2010) [2]. *A. citrulli* infects plants via stomata or wounds, leading to seedling blight and fruit rot (Burdman & Walcott, 2012) [8]. The bacterium polar flagella contribute to its virulence both before and after host tissue penetration, with motile cells observed in the xylem sap of infected plants (Bahar *et al*., 2011). The bacterium pathogenesis occurs through infection via stomata or wounds, resulting in significant economic losses due to reduced yields and diminished fruit marketability (Zhao & Walcott, 2018) [43]. *A. citrulli* strains are divided into two genetically distinct groups, with group II strains being more aggressive on watermelon. The bacterium relies on a type III secretion system for pathogenicity, with recent research revealing that *A. citrulli* strains possess over 60 type III effector genes, approximately 15% of which are group-specific. Despite its economic importance, management strategies for BFB are limited, and there are no reliable sources of resistance, highlighting the need for continued research to develop effective control measures (Bahar & Burdman, 2010) [2].

The economic and ecological consequences *of A. citrulli* are significant. BFB significantly impacts global cucurbit production, with outbreaks leading to severe crop losses and jeopardizing food security in key agricultural areas. Additionally, the ramifications of this disease go beyond immediate losses, as infected fruits cannot be sold, negatively affecting farmer's livelihoods and the sustainability of agriculture (Shrestha, *et al*., 2013; Popovic & Ivanovic, 2015) [37].

This review explores the genetic diversity of *Acidovorax citrulli*, which plays a critical role in its adaptability, virulence, and resistance to various control strategies. A profound comprehension of the genetic factors underpinning its pathogenicity is essential for formulating effective management approaches that integrate cultural, chemical, biological, and genetic strategies. The primary objectives of this review are to elucidate the mechanisms that promote genetic variability in *A. citrulli*, examine its interactions with host organisms, and evaluate the implications of these dynamics for sustainable management practices. Furthermore, our analysis underscores the significance of novel tools and technologies, such as whole-genome sequencing and CRISPR gene editing, transforming our capacity to address this pathogen. This review aspires to advance sustainable agricultural practices and bolster food security by connecting fundamental research with practical applications. The insights gained from understanding *A. citrulli* at the genetic level will pave the way for innovative solutions to mitigate its impact on crop production.

Materials and Methods

This review consolidates a wide range of findings derived from an extensive evaluation of peer-reviewed journal articles, scholarly books, and relevant conference proceedings that focus on *Acidovorax citrulli* and its management. The research approach involved thorough searches across reputable electronic databases, including PubMed, Scopus, Web of Science, and Google Scholar. The selection process utilized targeted keywords such as "*Acidovorax citrulli*," "genetic diversity," "bacterial fruit blotch," "cucurbits," "pathogenesis," and "management strategies," aiming to pinpoint the most significant studies in this domain.

To ensure the relevance and currency of the information, inclusion criteria were established to prioritize research published within the last twenty years. This focus allowed for the assimilation of the latest scientific advancements and breakthroughs in understanding *Acidovorax citrulli*. Notably, studies that employed advanced genomic techniques such as whole-genome sequencing (WGS), multi-locus sequence typing (MLST), and CRISPR methodologies were emphasized for their critical role in elucidating genetic diversity and enhancing pathogen management approaches.

Furthermore, the review incorporates a variety of case studies and experimental results that examine the effectiveness of biological control agents, cultural management practices, and integrated pest management (IPM) techniques. Through careful collation, analysis, and synthesis of data, this work highlights significant trends, identifies research gaps, and suggests promising avenues for future investigation. To provide a comprehensive understanding of the topic, cross-referencing among sources was meticulously conducted, reinforcing the validity of the findings.

Where applicable, statistical data and graphical representations from the original studies have been integrated to illustrate key points clearly. In adherence to ethical standards, all sources have been properly cited, and copyright guidelines concerning figures and data use have been diligently followed. This review aims to serve as a valuable resource for researchers and practitioners seeking to deepen their understanding of *Acidovorax citrulli* and improve management strategies.

Genetic Diversity of *Acidovorax citrulli*

1. Overview of Genetic Variability

Acidovorax citrulli is a gram-negative bacterium that causes bacterial fruit blotch (BFB) in cucurbits, posing significant threats to agricultural productivity. Its genomic structure, characterized by a relatively small circular chromosome, encodes genes vital for pathogenicity and survival under diverse environmental conditions (Burdman and Walcott, 2012) [8]. The bacterium exhibits remarkable genetic variability, driven by evolutionary processes and adaptation to different hosts. Historically, strains of *A. citrulli* have been classified into two main groups, Group I and Group II, based on their host preference and genetic differences. Group I strains predominantly infect non-watermelon hosts, whereas Group II strains are primarily associated with watermelon, underscoring host-specific adaptations (Zivanovic & Walcott, 2017) [44].

2. Mechanisms Driving Genetic Diversity

Horizontal gene transfer (HGT) plays a crucial role in the genetic diversification of *A. citrulli*, allowing the organism to acquire novel genes from other microorganisms. This process enriches its genomic repertoire, enhancing both pathogenicity and environmental adaptability (Liu *et al*., 2014) [29]. Additionally, mutation rates contribute to variability by introducing genetic changes that may provide selective advantages under specific environmental pressures. Factors such as host immune responses and agricultural practices shape the evolutionary trajectory of *A. citrulli* populations, promoting the development of traits that enhance survival and virulence. Moreover, host-pathogen interactions are essential drivers of genetic diversity (Yadav, *et al*., 2020) [41]. The ongoing arms race between *A. citrulli* and its plant hosts fosters co-evolutionary dynamics, where the pathogen evolves tactics to bypass host defenses, while hosts concurrently develop resistance mechanisms (Schroeder, *et al*., 2017) [34]. These interactions highlight the importance of understanding pathogen diversity to inform sustainable management practices.

3. Tools for Genetic Analysis

Advances in molecular tools have revolutionized the study of *A. citrulli* genetic diversity. Whole-genome sequencing (WGS) provides comprehensive insights into the bacterium's genomic organization and evolutionary history, enabling precise identification of genes associated with virulence and host specificity (Bryant, *et al*., 2012) [7]. Multi-locus sequence typing (MLST) has been widely employed to categorize strains and investigate epidemiological patterns, facilitating the tracing of outbreaks and understanding transmission dynamics (Dunne *et al*., 2018) [12]. Phylogenetic analyses, often integrated with WGS data, enable the construction of evolutionary relationships among strains, offering valuable insights into the origins and spread of pathogenic lineages (Klemm and Dougan, 2016) [26]. Furthermore, CRISPR-based technologies are emerging as powerful tools for diagnostics and functional characterization of *A. citrulli*. These methods enhance the resolution of genetic studies and hold promise for rapid, field-deployable diagnostics (Tanny, *et al*., 2023) [39].

Pathogenesis and Host Interaction

1. Mechanisms of Infection

Virulence factors such as the Type III secretion system (T3SS) are central to the pathogenicity of *Acidovorax citrulli*. The T3SS facilitates the translocation of effector proteins into host cells, disrupting cellular processes and promoting bacterial colonization (Burdman *et al*., 2014). Additionally, adhesion mechanisms enable *A. citrulli* to attach to the surfaces of cucurbit tissues, a critical first step in infection. The bacterium invades host tissues through stomata or wounds, establishing infection and spreading systemically (Melotto *et al*, 2008) [31].

2. Host Susceptibility and Resistance

The genetic basis of resistance in cucurbit species is a focal area of research aimed at mitigating the impact of BFB. Resistance genes in certain cucurbit varieties have been identified, offering promising avenues for breeding resistant cultivars (Leibman *et al*., 2018). However, the effectiveness of resistance is often compromised by the rapid evolution of *A. citrulli* populations.

Host immune responses also play a pivotal role in shaping pathogen evolution. Pattern recognition receptors (PRRs) in cucurbits detect pathogen-associated molecular patterns (PAMPs), triggering immune responses that limit infection. Nonetheless, *A. citrulli* counteracts these defenses through effector proteins that suppress host immunity, highlighting the dynamic interplay between host and pathogen (Gong & Xin, 2021) [17].

Management Strategies

1. Cultural Practices

Acidovorax citrulli, the causal agent of bacterial fruit blotch (BFB), poses a significant threat to cucurbit crops worldwide (Burdman & Walcott, 2012) [8]. The pathogen is primarily seed-borne and seed-transmitted, facilitating its global spread through international seed trade (Zhao & Walcott, 2018) [43]. Effective management of BFB relies on accurate detection methods in seed lots, with DNA extraction and purification being critical for robust PCR analysis (Giovanardi *et al*., 2015) [16]. Cultural practices play a crucial role in controlling BFB, particularly in nurseries. Sub-irrigation combined with bactericidal sprays at the cotyledon stage can significantly reduce disease spread, as cotyledons are the main source of secondary infection (Chalupowicz *et al*., 2015). While various seed treatment methods have been explored, complete eradication of *A.*

citrulli from contaminated seeds remains challenging (Giovanardi *et al*., 2015) [16]. The development of sensitive detection techniques and improved management strategies is essential for mitigating the economic impact of BFB on the cucurbit industry.

2. Chemical Controls

Chemical control of *Acidovorax citrulli*, remains challenging due to limited efficacy and resistance development (Husni *et al*., 2021) [22]. High-throughput screening has identified promising small molecules with bactericidal or bacteriostatic effects against *A. citrulli*, including thiamphenicol, nadifloxacin, pipemidic acid, ciclopirox, and zinc pyrithione (Lu *et al*., 2020). These compounds showed potential in reducing seed-to-seedling transmission of *A. citrulli*. Bacteriophages have also demonstrated efficacy as biocontrol agents, with phages ACP17 and ACPWH exhibiting broad-spectrum activity against *A. citrulli* strains (Hopkins *et al*., 2009; Rahimi & Choi, 2020) [21, 33]. In citrus disease management, insecticides are widely used to control vectors like the Asian *citrus psyllid*, while antibiotics are employed to suppress huanglongbing symptoms (Boina & Bloomquist, 2014) [5]. Area-wide management strategies and rotation of insecticides with different modes of action are crucial for sustainable control and mitigating resistance development.

3. Biological Control

Biological control strategies have shown promise in managing *Acidovorax citrulli* in cucurbits. *Rhizobacteria* like *Paenibacillus polymyxa* and *Sinomonas atrocyanea* can suppress *A. citrulli* and promote plant growth (Adhikari *et al*., 2017) [1]. Nonpathogenic *A. citrulli* strains, such as AAC00-1ΔhrcC, have proven effective as seed treatments, reducing BFB transmission by up to 81.8% (Johnson *et al*., 2011) [23]. Additionally, blossom protection using biocontrol agents like *Acidovorax avenae* subsp. *avenae* (AAA 99-2) and *Pseudomonas fluorescens* (A506) can significantly reduce seed infestation by *A. citrulli* (Fessehaie & Walcott, 2005) [14]. These biological control methods offer promising alternatives to chemical controls for managing BFB in cucurbit production.

4. Genetic Approaches

Breeding cucurbit crops for resistance to BFB is a long-term strategy to mitigate losses caused by *A. citrulli*. Recent advances in genomic research and molecular breeding techniques have significantly impacted the development of cucurbit crops resistant to bacterial fruit blotch (BFB), caused by *Acidovorax citrulli*. Genomic sequencing and bioinformatics have facilitated gene identification and understanding of genetic variation in Cucurbitaceae, enabling more effective molecular breeding strategies (Xu *et al*., 2024) [40]. The application of gene editing technologies, particularly CRISPR/Cas9, has shown promise in improving cucurbit crop resistance to diseases like BFB (Feng *et al*., 2023) [13]. These techniques allow for precise genetic modifications and overcome the limitations of conventional breeding methods. Integration of next-generation sequencing, omics approaches, and high-throughput genotyping methods has enhanced the identification of quantitative trait loci for key agronomic traits, including disease resistance (Xu *et al*., 2024) [40].

5. Integrated pest management approaches and their effectiveness

Effective management strategies for controlling *Acidovorax citrulli*, necessitate a multifaceted approach incorporating genetic and agronomic practices. Developing resistant cultivars through traditional breeding or genetic engineering offers a sustainable long-term solution, as demonstrated by ongoing research into plant genetic diversity that reveals viable resistance traits (Chaudhary *et al*., 2024) [11]. In addition, employing integrated pest management (IPM) practices can mitigate the pathogen impact. Methods such as crop rotation, proper sanitation, and the introduction of biocontrol agents which exhibit broad-spectrum antimicrobial activity, provide notable advances in sustainable control strategies (Scortichini, 2022) [35]. Furthermore, understanding the pathogen epidemiology and its interactions within the ecosystem is crucial for effectively predicting outbreaks and timing management interventions, thereby maximizing crop resilience against this insidious threat. Such a comprehensive framework highlights the importance of combining genetic insights with practical management tools. Integrated pest management (IPM) approaches have emerged as fundamental strategies for mitigating the impact of plant pathogens like *Acidovorax citrulli* while promoting sustainable agricultural practices (Bigirimana *et al*., 2016) [4]. By incorporating biological, cultural, physical, and chemical controls, IPM systems offer a multifaceted response to pest threats, thus minimizing reliance on chemical pesticides. Studies show that effective implementation of IPM can reduce disease incidence significantly, specifically in crops such as cucurbits, where insect-vectored bacterial pathogens are prevalent (Chandi, 2021) [10]. Innovative methods, such as tailored seed treatments to inhibit seed-borne infections, are also pivotal in IPM frameworks (Kalbande & Yadav, 2021) [25]. Therefore, the effectiveness of IPM lies not only in its comprehensive management strategies but also in its adaptability to various agricultural contexts, which is critical in promoting long-term sustainability in crop production.

Challenges and Future Directions

1. Challenges

The limited availability of genetic information regarding specific strains of *Acidovorax citrulli* presents a considerable challenge in fully understanding and managing the diversity of this pathogen. The situation is exacerbated by the emergence of new virulent strains, which can potentially circumvent current control measures. Furthermore, environmental and regulatory barriers can impede the implementation of novel management strategies, highlighting the need for innovative and flexible approaches to address these complexities (Jones, 2017) [24].

2. Research Gaps

There is an urgent requirement for international collaborative genetic databases to unify and exchange information regarding *A. citrulli* strains. These resources would improve our capacity to forecast outbreaks and formulate specific management strategies. Additionally, investigating non-host interactions might reveal alternative methods to control *A. citrulli*, leading to innovative perspectives on ecosystem-based management approaches (Smith *et al*., 2007) [38].

3. Prospective Advances

Artificial intelligence (AI) is increasingly recognized as a revolutionary tool in predicting disease outbreaks and distinguishing between various strains of *Acidovorax citrulli*. By employing machine learning algorithms, researchers can systematically analyze intricate datasets to uncover patterns that enable precise forecasting of pathogen behavior. Furthermore, the advancement of next-generation resistant crops through innovative breeding techniques and gene-editing methodologies presents a significant opportunity for enhancing sustainability in agricultural practices (Hamdan *et al*., 2022) [19].

Future directions for research and sustainable practices in pathogen control

Looking to the future, the combination of advanced genomic techniques and environmentally friendly practices will play a vital role in improving our understanding and management of *Acidovorax citrulli* and similar plant pathogens. Research efforts should concentrate on investigating the genetic diversity within these pathogen populations to uncover resilient traits that can survive under various environmental pressures. Moreover, the use of biocontrol agents, such as microbial antagonists and beneficial bacteria, offers a sustainable alternative to conventional chemical pesticides. This strategy not only helps maintain ecological balance but also minimizes negative effects on the environment. Embracing precision agriculture methods, including monitoring systems with sensors, can allow for timely and focused interventions, enhancing resource efficiency and reducing the spread of pathogens. In addition, collaboration among researchers, farmers, and policymakers is crucial for creating integrated pest management strategies that emphasize sustainable practices. By merging these innovative methods, we can develop agricultural systems that are robust enough to ensure food security in light of the challenges posed by climate change and adaptable pathogens.

Conclusion

This review highlights the significant genetic diversity of *Acidovorax citrulli* and its implications for pathogenesis and management. Understanding the mechanisms driving genetic variability and the tools available for genetic analysis has been pivotal in informing current strategies. Management approaches that integrate cultural practices, chemical and biological controls, and genetic innovations offer the best prospects for sustainable control of bacterial fruit blotch. To address future challenges, it is essential to integrate genetic insights into agricultural practices and promote interdisciplinary collaboration. The convergence of cutting-edge technologies such as AI and CRISPR with traditional breeding and management practices will pave the way for innovative solutions. Ultimately, achieving sustainable agriculture in the face of evolving pathogens requires a concerted effort across scientific disciplines and stakeholder communities.

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