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Genomic Architecture of *Bacillus thuringiensis*: Insights into Functional Elements

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Abstract *Bacillus thuringiensis* (Bt) is a Gram-positive bacterium renowned for its insecticidal properties, primarily due to the production of Cry and Cyt toxins. This systematic review delves into the genomic architecture of Bt, highlighting the functional elements that contribute to its efficacy as a biopesticide. The study synthesizes findings from various studies to provide a comprehensive understanding of the structural and functional aspects of Bt toxins, including the novel Vpb4Da2 protein with its unique six-domain architecture and receptor-binding regions, the broad-spectrum insecticidal activity of multiple Cry proteins, and the innovative use of chimeric proteins to enhance pest control. Additionally, the study explores the potential of Bt as a biofertilizer and its role in promoting plant growth while controlling phytopathogens. The insights gained from this study could pave the way for the development of more effective and sustainable pest management strategies.

Keywords *Bacillus thuringiensis*; Cry toxins; Vpb4Da2 protein; Bioinsecticide; Genomic architecture

1 Introduction

Bacillus thuringiensis (Bt) is a Gram-positive, spore-forming bacterium that is widely recognized for its insecticidal properties. It produces parasporal crystal proteins, known as Cry and Cyt toxins, during sporulation, which are highly toxic to a variety of insect larvae upon ingestion (Dorsch et al., 2002; Barbosa et al., 2015; Reyaz et al., 2019). These toxins have been extensively utilized in agricultural pest control as biopesticides, offering an environmentally friendly alternative to chemical insecticides (Nair et al., 2020). The bacterium's ability to produce a diverse array of toxins has made it a subject of significant interest in the field of integrated pest management (Crickmore et al., 2020).

Understanding the genomic architecture of Bt is crucial for several reasons. Firstly, it allows for the identification and characterization of the genes responsible for its insecticidal properties, which can lead to the development of more effective biopesticides. Secondly, it provides insights into the genetic diversity and evolutionary mechanisms that enable Bt to adapt to different environmental conditions and host species (Barbosa et al., 2015). Additionally, knowledge of the genomic structure, including the presence of plasmids and their associated genes, can inform strategies for genetic engineering to enhance the bacterium's efficacy and spectrum of activity (Li et al., 2017; Crickmore et al., 2020).

The study aims to provide a comprehensive overview of the current understanding of the genomic architecture of *Bacillus thuringiensis*. This includes an analysis of the functional elements within its genome, such as the coding sequences for Cry and Cyt toxins, and other virulence factors. The study hopes to synthesize findings from recent genomic studies to highlight the genetic basis of Bt's insecticidal properties and its potential applications in biocontrolmize the use of Bt in pest management.

2 Overview of Bt Genomic Structure

Bacillus thuringiensis (Bt) is a gram-positive, spore-forming bacterium widely recognized for its insecticidal properties, primarily due to the production of crystal proteins (Cry and Cyt toxins). The genomic architecture of Bt is complex, comprising a circular chromosome and multiple plasmids that harbor genes responsible for its pathogenicity and adaptability (Figure 1) (Zhou et al., 2024).

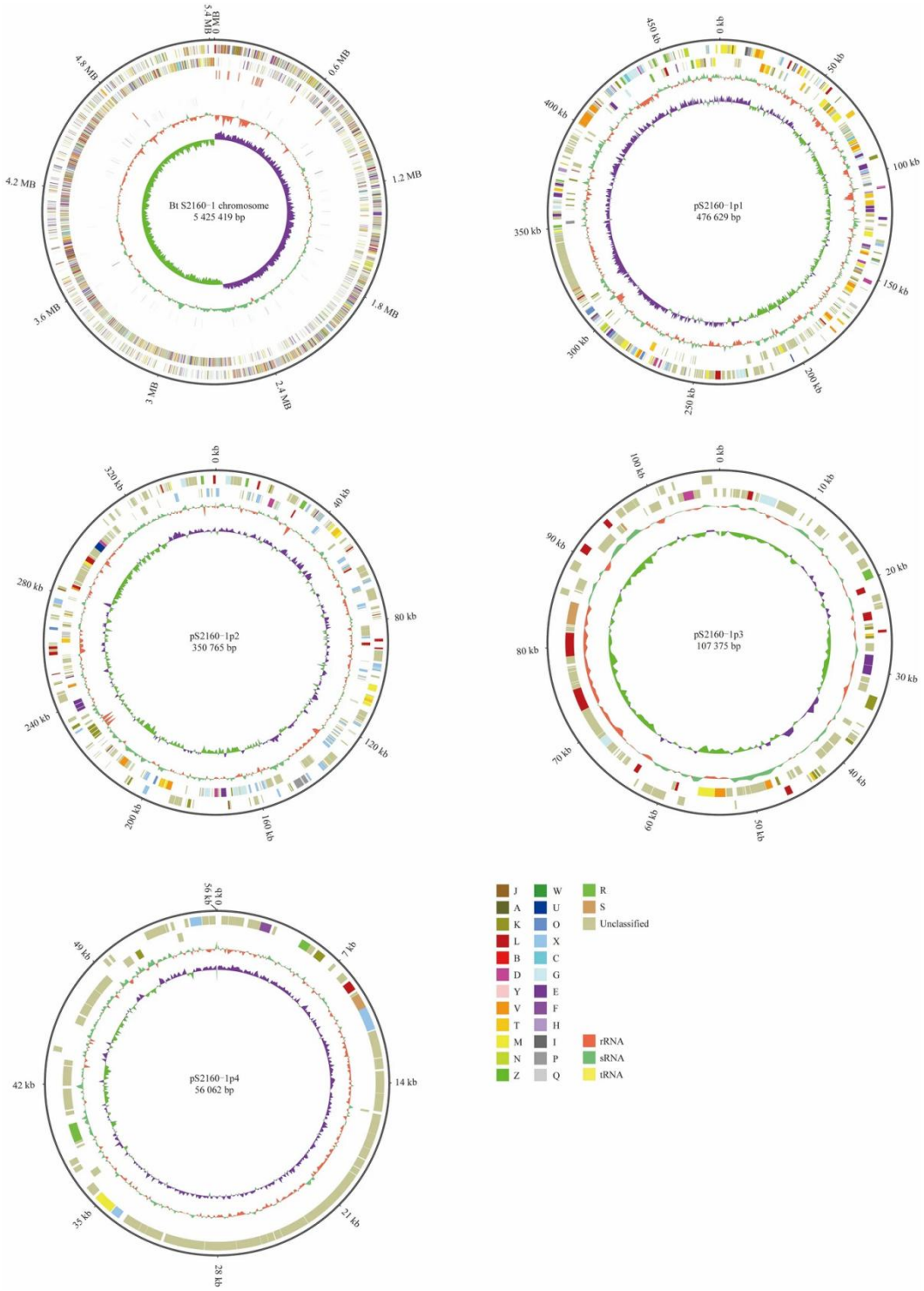

Figure 1 Visual map of the complete genome of Bt S2160-1 (Adopted from Zhou et al., 2024)

2.1 Genome size and composition

The genome size of Bt varies among different strains, typically ranging from approximately 5 to 6.5 million base pairs (bp). For instance, the genome of Bt isolate T414 is 6 493 494 bp in length, containing 6 877 coding sequences and 152 RNAs (Reyaz et al., 2019). Similarly, the genome of Bt strain BM-BT15426 is 5 246 329 bp long, with 5 409 predicted genes and an average G+C content of 35.40% (Liu et al., 2017). These genomes encode a variety of virulence factors, including insecticidal crystal proteins, chitinases, proteases, and hemolysins, which contribute to the bacterium's entomopathogenic capabilities (Reyaz et al., 2019).

2.2 Chromosomal organization

The chromosomal organization of Bt is characterized by a single circular chromosome that encodes essential genes for the bacterium's survival and pathogenicity. For example, the complete genome sequence of Bt HER1410 reveals a circular chromosome that contains a unique cry gene, cry1Ba4, located in a genomic island near the chromosome replication origin (Figure 2) (Lechuga et al., 2020a). This chromosomal arrangement is crucial for the regulation of gene expression and the maintenance of genomic stability. Additionally, the chromosome often contains genes involved in metabolic pathways, antibiotic resistance, and other essential cellular functions (Liu et al., 2017; Lechuga et al., 2020a).

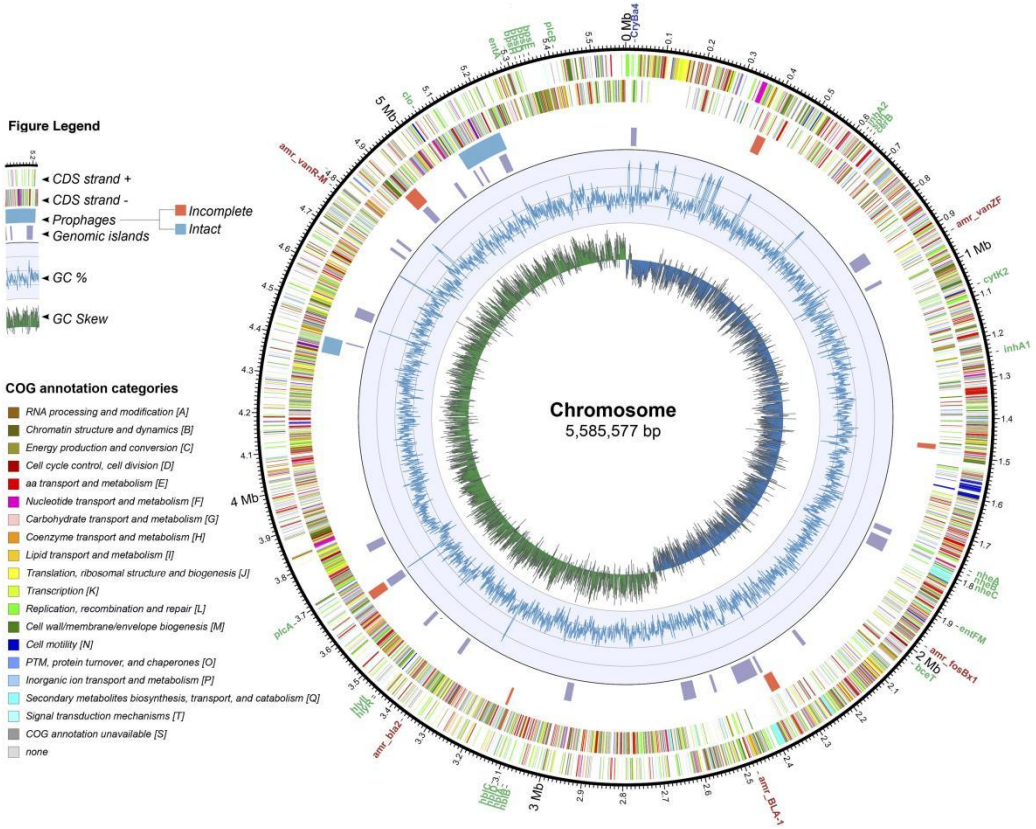

Figure 2 Circular representation of *B. thuringiensis* HER1410 chromosome (Adopted from Lechuga et al., 2020a)

2.3 Plasmid content

Plasmids play a significant role in the genomic architecture of Bt, often carrying genes that encode insecticidal toxins and other virulence factors. The number and size of plasmids can vary widely among different Bt strains. For instance, Bt strain HD521 contains six circular plasmids, while strain HS18-1 has nine circular plasmids (Sun et al., 2021). These plasmids encode various virulence proteins, including Cry and Vip toxins, which are critical for the bacterium's insecticidal activity (Sun et al., 2021). In Bt GR007, three megaplasmids were identified, with the largest two (pGR340 and pGR157) containing multiple pesticidal protein genes, such as *cry* and *vip* genes (Pacheco et al., 2021). Similarly, Bt HER1410 harbors two megaplasmids, pLUSID1 and pLUSID2, which are involved in virulence and sporulation processes, respectively (Lechuga et al., 2020a).

The presence of plasmids also facilitates horizontal gene transfer, contributing to the genetic diversity and adaptability of Bt. For example, the comparative genomics of Bt subsp. *israelensis* revealed active plasmid exchange among strains, highlighting the dynamic nature of plasmid content in this species (Bolotin et al., 2017). This exchange of genetic material allows Bt to acquire new traits, such as resistance to environmental stresses and enhanced pathogenicity, thereby increasing its ecological fitness and effectiveness as a biopesticide (Bolotin et al., 2017; Méric et al., 2018).

In summary, the genomic structure of *Bacillus thuringiensis* is characterized by a circular chromosome and multiple plasmids, which together encode a wide array of genes responsible for the bacterium's insecticidal properties and adaptability. The variability in genome size, chromosomal organization, and plasmid content among different Bt strains underscores the genetic diversity and evolutionary potential of this important biopesticide.

3 Functional Elements in the Bt Genome

3.1 Protein-coding genes

Bacillus thuringiensis (Bt) is renowned for its diverse array of protein-coding genes, particularly those encoding insecticidal proteins. The genome of Bt isolate T414, for instance, contains numerous protein-coding sequences, including genes for parasporal crystal proteins such as *cry1Aa*, *cry1Ab*, *cry1Ac*, *cry1IAa*, *cry2Aa*, *cry2Ab*, and *cyt1*, as well as the vegetative insecticidal protein gene vip3Aa. These genes are primarily plasmid-borne, located on plasmids p414A and p414E (Reyaz et al., 2019). Similarly, the Bt GR007 strain harbors multiple pesticidal protein genes, including 10 *cry* genes (e.g., *cry1Ab*, *cry1Bb*, *cry1Da*) and two *vip* genes (*vip3Af* and *vip3Ag*), distributed across its chromosome and three megaplasmids (Pacheco et al., 2021). These protein-coding genes are crucial for Bt's biopesticidal properties, enabling it to target a wide range of insect pests.

3.2 Regulatory elements

Regulatory elements in the Bt genome play a pivotal role in the expression and regulation of its protein-coding genes. These elements include promoters, enhancers, and other sequences that control the transcription and translation of genes. The presence of these regulatory elements ensures that the insecticidal proteins are produced in response to specific environmental cues, optimizing the bacterium's effectiveness as a biopesticide. For instance, the intrinsic promoters associated with the Cry proteins in Bt GR007 facilitate the expression of these proteins in an acrystalliferous strain, demonstrating the importance of regulatory elements in gene expression (Pacheco et al., 2021).

3.3 Non-coding RNAs

Non-coding RNAs (ncRNAs) are another significant component of the Bt genome, contributing to the regulation of gene expression and adaptation to environmental changes. A comparative study of ncRNAs in *Bacillus cereus* sensu lato, which includes Bt, revealed a diverse set of ncRNAs across different strains. The most prevalent functional category of ncRNAs was Cis-reg, with Riboswitch being the most frequent class in chromosomes, while Group II introns were more common in plasmids (Gonçalves et al., 2021). The wide distribution and diversity of ncRNAs in Bt suggest their role in enhancing the bacterium's adaptability and regulatory capabilities, which are essential for its survival and efficacy as a biopesticide.

4 Toxin Genes and Their Organization

4.1 Cry and Cyt toxin genes

Bacillus thuringiensis (Bt) produces a variety of Cry and Cyt toxins, which are crucial for its insecticidal properties. Cry toxins, such as Cry4Aa, Cry4Ba, Cry10Aa, and Cry11Aa, and Cyt toxins, such as Cyt1Aa and Cyt2Ba, are particularly effective against mosquito larvae (Pérez et al., 2005; Fernández-Luna et al., 2010). The Cry toxins function by binding to specific receptors in the insect midgut, leading to pore formation and cell lysis (Pardo-López et al., 2013). Cyt toxins, on the other hand, can act as receptors for Cry toxins, enhancing their binding and toxicity (Pérez et al., 2005). For instance, Cyt1Aa has been shown to synergize with Cry11Aa by functioning as a membrane-bound receptor, thereby overcoming insect resistance (Pérez et al., 2005).

4.2 Gene clusters and operons

The genes encoding Cry and Cyt toxins are often organized in clusters and operons, facilitating their coordinated expression. For example, the *cryIVD* and *cytA* genes are located within a 9.4-kb HindIII fragment and are co-expressed in *Bacillus thuringiensis*, leading to synergistic toxicity against mosquito larvae. Additionally, novel strains of Bt, such as the H3 strain, have been found to carry multiple Cry toxin genes organized in a dynamic

plasmid environment, which includes mobile genetic elements that contribute to the genetic diversity and adaptability of the bacterium (Fayad et al., 2020). This organization allows for the efficient production of multiple toxins, enhancing the overall insecticidal activity.

4.3 Regulatory mechanisms of toxin genes

The expression of Cry and Cyt toxin genes is tightly regulated to ensure their effective production during sporulation. Various regulatory proteins and environmental factors influence the transcription of these genes. For instance, the presence of a 20-kDa protein has been shown to enhance the production of CytA protein in Escherichia coli, although it is not required in *Bacillus thuringiensis*. Additionally, the interaction between Cry and Cyt toxins can be modulated by specific mutations in their receptor-binding domains, which affect their binding affinity and synergistic interactions (Lailak et al., 2013). Understanding these regulatory mechanisms is crucial for optimizing the production of Bt toxins and improving their efficacy as bioinsecticides.

5 Virulence Factors and Pathogenicity Islands

5.1 Identification of virulence genes

Virulence genes in *Bacillus thuringiensis* (Bt) are crucial for its pathogenicity and are often located on mobile genetic elements such as plasmids and transposons. For instance, the study by (Wang et al., 2008) identified a locus in a virulence-attenuated Bt mutant that encodes 29 potential protein-coding ORFs, many of which share homology with genes on the plasmid pE33L466 of *Bacillus cereus*. This locus includes mobile elements like the transposon Tn4430, which plays a significant role in Bt virulence during *Manduca sexta* infection. Additionally, the yqgB and yqfZ genes have been identified as important for Bt's pathogenicity, as their simultaneous inactivation results in attenuated virulence against Bombyx mori larvae (Wang et al., 2008).

5.2 Pathogenicity islands

Pathogenicity islands (PAIs) are distinct genetic elements that encode various virulence factors and are typically absent in non-pathogenic strains. PAIs are a subclass of genomic islands acquired through horizontal gene transfer and contribute significantly to the virulence of bacterial pathogens (Gal-Mor and Finlay, 2006). In Bt, PAIs have been identified that contain genes encoding pesticidal proteins and other virulence factors. For example, the complete genome sequencing of Bt GR007 revealed multiple pesticidal protein genes located on megaplasmids, which are likely part of PAIs (Pacheco et al., 2021). These PAIs contribute to the rapid evolution and diversification of Bt, enabling it to adapt to different hosts and environments (Desvaux et al., 2020).

5.3 Horizontal gene transfer

Horizontal gene transfer (HGT) is a key mechanism in the evolution of microbial genomes, including the acquisition of virulence factors in Bt. HGT allows for the transfer of PAIs and other mobile genetic elements between different bacterial species, facilitating the spread of virulence genes (Dobrindt et al., 2004). The study of the conjugative plasmid pAW63 in the *Bacillus cereus* group, which includes Bt, has provided insights into the genesis of virulence plasmids such as pXO2 in *Bacillus anthracis* and pBT9727 in Bt. These plasmids share a common backbone and exhibit regions of high sequence plasticity, indicating their evolution through HGT (Auwera et al., 2005). Additionally, the presence of mobile elements like transposons and insertion sequences in Bt further supports the role of HGT in its virulence (Wang et al., 2008).

In summary, the identification of virulence genes, the role of pathogenicity islands, and the impact of horizontal gene transfer are critical components in understanding the genomic architecture and pathogenicity of *Bacillus thuringiensis*. These elements collectively contribute to the bacterium's ability to cause disease and adapt to various environments.

6 Mobile Genetic Elements

6.1 Plasmids

Plasmids play a crucial role in the genetic architecture of *Bacillus thuringiensis* (Bt), contributing to its adaptability and pathogenicity. The modular genetic architecture of plasmids such as pIS56-63, which harbors the cry1Ab21 gene, highlights their role in toxin production and gene transfer. This plasmid is composed of four functional modules: a mobile insertion cassette, a putative conjugative element, a regulation sequence, and a

replicon, indicating a complex structure resulting from recombination events (Murawska et al., 2014). Additionally, the complete genome sequence of Bt HER1410 revealed two megaplasmids, pLUSID1 and pLUSID2, which are involved in virulence and potentially sporulation, respectively (Lechuga et al., 2020a; Lechuga et al., 2020b). The presence of a cryptic rolling-circle replicating plasmid, pGI2, further underscores the diversity of plasmid types in Bt, with its modular organization and mobilization capabilities6. Comparative genomics studies have also shown active plasmid exchange among Bt strains, contributing to genetic diversity and adaptability (Bolotin et al., 2017).

6.2 Transposons

Transposons are another significant component of the mobile genetic elements in Bt. The insertion sequence IS231, identified in Bt strain berliner 1715, exemplifies the structural organization typical of transposons, with inverted repeats and a long open reading frame encoding a putative transposase. The presence of transposons like Tn4430 in plasmids such as pGI2 highlights their role in genetic rearrangements and horizontal gene transfer. Additionally, the identification of IS240-like and IS150-like elements in Bt ssp. *fukuokaensis* further illustrates the diversity of transposable elements and their potential impact on gene regulation and mobility. The dynamic nature of transposons is evident in the highly mobile genetic environment of plasmids like pH3-180, which carry multiple novel insertion sequences and class II transposable elements (Fayad et al., 2020).

6.3 Integrons and insertion sequences

Integrons and insertion sequences (IS) are integral to the genetic plasticity of Bt. The IS231 element, the first identified IS element in Bt, shares structural homology with the Escherichia coli IS4 element, suggesting a conserved mechanism of transposition. The presence of IS elements like IS240 and IS150 in Bt plasmids indicates their role in gene capture and dissemination. The complete sequence of plasmids such as pFR55 from Bt INTA-FR7-4 reveals a near-complete conjugation apparatus and extensive homology with other Bt plasmids, highlighting the role of IS elements in plasmid evolution and function (Amadio et al., 2009). The identification of mobile genetic elements in plasmids like pAW63, which shares homology with the virulence plasmid pXO2 of *Bacillus anthracis*, further underscores the evolutionary significance of integrons and IS elements in shaping the genetic landscape of Bt (Auwera et al., 2005).

7 Genomic Variability and Evolution

7.1 Strain-specific genetic variation

Bacillus thuringiensis (Bt) exhibits significant strain-specific genetic variation, which is crucial for its adaptability and effectiveness as a biocontrol agent. Studies have shown that different Bt strains possess unique genetic elements that contribute to their specific ecological niches and host interactions. For instance, the genomes of Bt strains MYBT18246, MYBT18247, and MYBT18679 contain approximately 15% to 20% genetic material encoding elements related to genome plasticity, such as virulence factors and mobile genetic elements like bacteriophages and transposases (Hollensteiner, 2017). Additionally, the RAPD technique has revealed distinct DNA patterns among various Bt isolates, indicating substantial genetic diversity even within local populations (Qasem et al., 2015).

7.2 Mechanisms of genetic diversity

The genetic diversity in Bt is driven by several mechanisms, including horizontal gene transfer, mobile genetic elements, and bacteriophages. Prophages, for example, play a significant role in the mobilization of chromosomally encoded cry-toxins, which are critical for Bt's pathogenicity (Hollensteiner, 2017). Comparative genomic analyses of phages and prophages from Bt strains have shown that these elements contribute to the genetic variability and evolutionary dynamics of the species. For instance, the phiCM3 phage and proCM3 prophage from Bt strain YM-03 exhibit high genomic similarity to other Bacillus phages, suggesting a common evolutionary origin and subsequent genome rearrangements (Yuan et al., 2014). Furthermore, multi-REP-PCR fingerprinting has demonstrated that Bt strains cluster into distinct groups based on their genomic profiles, reflecting their evolutionary relationships and genetic diversity (Cherif et al., 2007).

7.3 Evolutionary implications

The evolutionary implications of Bt's genomic variability are profound, influencing its adaptability, host range, and biocontrol efficacy. The coevolution of Bt with its hosts, such as Caenorhabditis elegans, has been shown to favor high virulence, with specific cry toxin genes sweeping to fixation in coevolving populations (Hollensteiner, 2017). This adaptive evolution is facilitated by the presence of mobile genetic elements and the ability to acquire new genetic material through horizontal gene transfer. Additionally, the genetic diversity among Bt strains allows for the development of specialized biocontrol agents with tailored properties for different agricultural applications. For example, the genomic analysis of Bt strain MORWBS1.1 has identified genes for the biosynthesis of biopesticidal metabolites, highlighting its potential as a candidate biocontrol agent (Adeniji et al., 2021). Overall, the genomic architecture of Bt underscores its evolutionary potential and versatility as a biocontrol organism.

8 Biotechnological Applications

8.1 Use in biopesticides

Bacillus thuringiensis (Bt) is widely recognized for its use as a biopesticide due to its ability to produce insecticidal crystal proteins (ICPs) that are toxic to a variety of insect pests. The genomic exploration of various Bt strains has revealed a plethora of pesticidal protein genes that contribute to its effectiveness as a biopesticide. For instance, the complete genome sequencing of Bt strain GR007 identified multiple pesticidal protein genes, including 10 *cry* genes and two *vip* genes, which are crucial for its toxicity against Spodoptera frugiperda and *Manduca sexta* larvae (Pacheco et al., 2021). Similarly, the genome of Bt serovar galleriae strain HD-29 harbors ten plasmids, with three large ones carrying eight insecticidal protein genes, making it highly toxic to Lepidoptera insect pests (Zhu et al., 2015). The novel Bt strain BLB406, with its unique combination of *cry* and *vip* genes, also shows potential as a bioinsecticide against Aedes aegypti larvae (Zghal et al., 2018). These findings underscore the significant role of Bt in sustainable pest management and its widespread use in agriculture (Gutiérrez et al., 2019; Lechuga et al., 2020a).

8.2 Genetic engineering for enhanced traits

Genetic engineering has been employed to enhance the traits of Bt strains, making them more effective and versatile in pest control. The genomic characterization of Bt strains has facilitated the identification and cloning of specific pesticidal protein genes for targeted expression. For example, the proteomic analysis of Bt GR007 revealed the expression of seven Cry proteins, each displaying differential toxicity against specific insect larvae (Pacheco et al., 2021). Additionally, the complete genome sequence of Bt HER1410 highlighted the presence of a unique cry gene located in a genomic island near the chromosome replication origin, which could be exploited for genetic engineering purposes (Lechuga et al., 2020b). Comparative genomic and proteomic analyses have also provided insights into the expression patterns of various insecticidal proteins, enabling the construction of highly virulent engineered bacteria (Rang et al., 2015). These advancements in genetic engineering hold promise for developing Bt strains with enhanced pesticidal properties and broader insecticidal spectra (Lechuga et al., 2020b).

8.3 Potential for industrial applications

Beyond its use in biopesticides, Bt has potential applications in various industrial sectors. The production of antimicrobial compounds by Bt strains, such as zwittermicin A, has been documented, indicating its potential use in the pharmaceutical industry (Adeniji et al., 2021). The complete genome sequence of Bt YBT-1518, which displays effective toxicity to nematodes, suggests its application in controlling nematode infestations in agriculture (Wang et al., 2014). Furthermore, the novel Bt strain YC-10, with its high toxicity to plant-parasitic nematodes, could be utilized in developing biocontrol agents for nematode management (Cheng et al., 2015). The unique combination of toxins in Bt strains, such as those found in BLB406, also points to potential anti-cancer activities, opening avenues for biomedical applications (Zghal et al., 2018). These diverse biotechnological applications of Bt highlight its versatility and potential for contributing to various industrial processes (Gutiérrez et al., 2019).

9 Concluding Remarks

The genomic architecture of *Bacillus thuringiensis* (Bt) has been extensively studied, revealing significant insights into its functional elements. Key findings include the identification of genes responsible for the biosynthesis of

biopesticidal metabolites, such as zwittermicin and various dioxygenases, which highlight the potential of Bt strains like MORWBS1.1 for biotechnological applications. The complete genome sequencing of multidrug-resistant strains, such as HM-311, has elucidated the presence of numerous antibiotic and heavy metal resistance genes, providing a reference for understanding the co-selection of resistance traits. Comparative genomic and proteomic analyses have shown that not all annotated genes are expressed, with some being silenced or expressed at very low levels, which is crucial for constructing highly virulent engineered bacteria. Additionally, the complete genome sequencing of various Bt strains has identified novel plasmids and unique cry genes, which are essential for the entomopathogenic properties of Bt.

Genomic studies in *Bacillus thuringiensis* are of paramount importance for several reasons. They provide a comprehensive understanding of the genetic basis for Bt's biopesticidal properties, which is critical for developing effective and sustainable pest control strategies. These studies help in identifying and characterizing resistance genes, which is essential for managing the spread of antibiotic and heavy metal resistance in agricultural and environmental settings. The comparative genomic and proteomic approaches enhance our ability to identify and manipulate key functional elements, thereby facilitating the development of genetically engineered Bt strains with improved efficacy and safety profiles. Lastly, the genomic data contribute to the taxonomic and phylogenomic classification of Bt, aiding in the accurate identification and differentiation of Bt strains from closely related species within the *Bacillus cereus* group.

Future research on the genomic architecture of *Bacillus thuringiensis* should focus on several key areas. Firstly, there is a need for more comprehensive comparative genomic studies to explore the diversity and distribution of biopesticidal genes across different Bt strains, which will aid in the identification of novel biocontrol agents. Secondly, further investigation into the mechanisms of gene silencing and low-level expression in Bt is necessary to optimize the expression of key insecticidal proteins and enhance the efficacy of Bt-based biopesticides. Thirdly, the role of plasmids and other mobile genetic elements in the horizontal transfer of resistance and virulence genes should be studied in greater detail to understand their impact on the evolution and adaptability of Bt. Additionally, integrating genomic data with functional studies, such as transcriptomics and proteomics, will provide a more holistic understanding of the regulatory networks and metabolic pathways in Bt. Finally, efforts should be made to develop standardized genomic and molecular markers for the accurate identification and classification of Bt strains, which will facilitate their use in both research and practical applications.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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