

Bacterial Secretion Systems: Molecular Mechanisms of Pathogenesis and Plant-Microbe Interactions

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ABSTRACT

The plant-pathogenic bacteria constitute a major problem for the agriculture sector in the world. They are equipped with highly advanced protein secretion systems that facilitate their ability to introduce virulence factors into plant cells and manipulate them in such a way that they can successfully colonize the plants. This review highlights the molecular architecture and biological role of bacterial secretion systems, especially focusing on their roles in phytopathogenesis. Gram-negative plant pathogens use various types of secretion systems, from the most basic Type I secretion system that is devoid of a periplasm step, through the more advanced Type II system, which is associated with priming of the classical secretory pathway, up to the highly complex Type III secretion system, which functions as a syringe to inject effector proteins directly into the cytoplasm of the target cells. Additionally, recent advances pertaining to other classes of bacterial secretion systems, specifically Types IV, V, and VI, will be comprehensively discussed.

Keywords: Bacterial Secretion Systems, Plant Pathogenic Bacteria, Effector Proteins, Type III Secretion System, Virulence Mechanisms

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1. INTRODUCTION

Crop loss by bacterial plant pathogens worldwide is greater than 220 million metric tons each year and causes considerable economic burden to farmers, posing threats to world food security. Some of the destructive bacteria that are known include Gram-negative bacteria such as *Pseudomonas*, *Ralstonia*, *Xanthomonas*, *Agrobacterium*, and *Erwinia*, which possess unique abilities to bypass plant defense

systems in order to successfully infect plants. Such unique ability of pathogenesis is facilitated by protein secretion systems, biological means through which virulence factors are secreted into the plant host cell. In contrast to Gram-positive bacteria, which utilize mainly the General Secretory (Sec) pathway and the Twin-Arginine Translocation (Tat) pathway for protein secretion across a single layer of cytoplasmic membrane, Gram-negative bacteria have a double-layered membrane system, thus making it more

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difficult for them to secrete proteins. These microorganisms have developed a range of secretion systems called Type I through Type VI (as well as the recent Type VII) secretion systems, each one being a unique system of protein secretion across cellular membranes. In order to understand the structure, energy, and function of such systems, it is possible to gain important information concerning bacterial pathogenic mechanisms, as well as develop new ways of disease management targeting such biological systems. In this review, the different secretion systems used by pathogenic bacteria infecting plants are considered with respect to their molecular functions, significance in disease development, and importance in plant pathology in agriculture. Through the understanding of the secretion systems used by pathogens to counter the plant immune system, there will be a scientific basis for devising interventions to combat these pathogens.

2. DISTINGUISHING EXTRACELLULAR PROTEINS FROM MEMBRANE-ASSOCIATED PROTEINS

Proteins in bacteria have different locations within the cell, each performing unique roles in infection and survival of bacteria. It is therefore important to understand such differences in order to comprehend how secretion systems operate. Secreted Extracellular Proteins (ECPs) are proteins that are excreted into the external environment and have

varied roles such as the enzymatic breakdown of host tissues, the use of toxins to damage host cells, and chemical messages used to communicate with host cells. They are soluble, freely floating proteins excreted via specific secretion systems and are key virulence factors in bacterial infections. Membrane-bound proteins, on the other hand, are permanently or temporarily bound to bacterial cell membranes. They include important transport, signal transduction, and energy metabolism transmembrane proteins, in addition to peripheral proteins with additional regulatory roles. In contrast to secreted proteins, they retain their important structural linkage with the lipid bilayer and are not distributed into the extracellular medium. Further to this, there is also production of extracellular polymeric substances (EPS), which are complex matrices that are predominantly made up of polysaccharides and have proteins, lipids, and nucleic acids as additives. Such matrices serve to protect bacterial colonies against any adverse environment as well as aiding in biofilm formation and survival of bacteria in an infectious state. The knowledge of such compartmentalization gives insights into the processes bacteria use to form virulent strategies.

3. OVERVIEW OF BACTERIAL SECRETION SYSTEMS IN PLANT PATHOGENS

There are different types of secretion systems used by plant pathogenic bacteria. The differences in these systems are outlined in the table below.

Table 1. Comparative Analysis of Bacterial Secretion Systems in Agricultural Pathogens

System	Gram Type	Key Organisms	Molecular Components	Substrates & Functions	Phytopathogenic Examples
T1SS	G+/G-	<i>E. chrysanthemi</i> , <i>Rhizobium</i>	ABC transporter, OMP, MFP	Proteases, toxins, metalloproteases	Pectate lyase, hemolysins in soft-rot <i>Erwinia</i>
T2SS	G-	<i>Xanthomonas</i> , <i>Ralstonia</i> , <i>Erwinia</i>	10-15 protein clusters, pseudopilus	Cellulases, pectinases, phosphatases	Plant cell wall-degrading enzymes, toxins
T3SS	G-	<i>Pseudomonas</i> , <i>Ralstonia</i> , <i>Xanthomonas</i>	>20 proteins (Hrp), needle complex	Effector proteins, immune suppression	<i>Pseudomonas syringae</i> Hop effectors, <i>Xanthomonas</i> XopX
T4SS	G+/G-	<i>Agrobacterium tumefaciens</i>	Pilus-like complex, channel proteins	T-DNA transfer, proteins, DNA-protein	T-DNA transfer to dicots, crown gall
T5SS	G-	<i>Xylella</i> , <i>Xanthomonas</i>	Autotransporter mechanism, β -barrel	Adhesins, proteases, β -harpin proteins	<i>Xylella fastidiosa</i> adhesins, biofilm formation
T6SS	G-	<i>Pseudomonas</i> , <i>Xanthomonas</i> , <i>Pectobacterium</i>	Phage-tail spike, Hcp/VgrG proteins	Effector injection, antimicrobial factors	<i>P. aeruginosa</i> antagonism, biofilm dynamics

4. TYPE I SECRETION SYSTEM: DIRECT MEMBRANE TRANSLOCATION

The Type I secretion system (T1SS) is a model for the most primitive bacterial secretion machinery, which involves transport of proteins across both bacterial membranes via a single ATP-driven process. This system involves three crucial elements: an ABC (ATP-binding cassette) transporter located within the inner membrane, which uses ATP energy to drive secretion; a membrane fusion protein (MFP), which connects the inner membrane with the outer membrane; and an outer membrane protein (OMP), which forms an exit pore. It is important to mention that T1SS-secreted substrates are C-terminally tagged with their secretion signals and are not localized to the periplasm, instead being released in their mature folded form. In bacteria involved in plant diseases, especially in soft-rot *Erwinia chrysanthemi* and *Rhizobium* species, T1SS-dependent secretion of hydrolytic enzymes and metalloproteases takes place, resulting in penetration into the plant cell wall by these proteins. Bacteria of the genus *Erwinia* secrete pectate lyases, which are responsible for hydrolysis of pectin, which is a vital structural element of the plant cell wall. This leads to the formation of maceration and decay of plant tissues known as soft-rot plant disease.

5. TYPE II SECRETION SYSTEM: SEC-PATHWAY DEPENDENT SECRETION

Secretion system Type II operates as a two-step process that is dependent on the first passage of the secreted protein through the conventional Sec secretion pathway. The substrates pass through the inner membrane of the bacteria as unfolded substrates by means of the Sec transport pathway. In the periplasmic space, the proteins fold into their mature conformation and then the Type II secretion system, which is a complex set of 10 to 15 proteins organized in a pilus-like structure, helps the protein cross the outer membrane barrier. *Xanthomonas campestris*, *Ralstonia solanacearum*, and *Erwinia carotovora* are some important plant pathogens that use the T2SS system to secrete a wide range of plant cell wall-degrading enzymes. *Xanthomonas* organisms secrete enzymes like cellulase, pectinase, and xylanase that work in collaboration to degrade the plant cell wall. *Ralstonia solanacearum*, the cause of bacterial wilt disease on millions of hectares all over the world, secretes different hydrolyzing enzymes. The secretion of these enzymes through the T2SS system is the major mechanism of virulence for these bacteria.

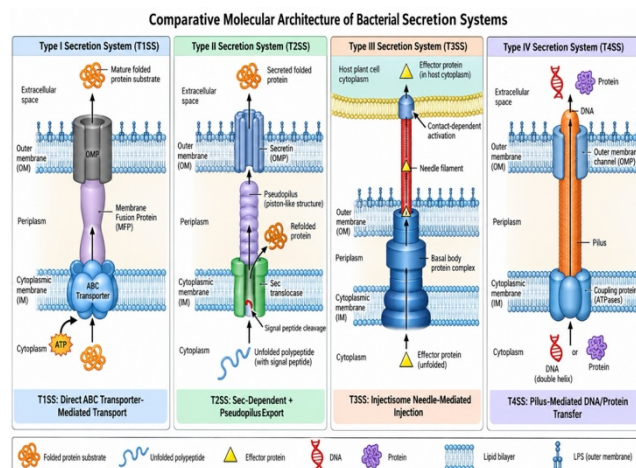


Figure 1. Comparative Molecular Architecture of Bacterial Secretion Systems

Schematic diagram representing the variations in structure between the type I, II, III, and IV secretion systems of Gram-negative bacteria. Type I secretion system crosses both membranes directly through an ABC transporter linkage. Type II secretion system first primes using the Sec pathway and then uses the pseudopilus pathway to cross the outer membrane. Type III secretes using an injectosome-like needle structure.

6. TYPE III SECRETION SYSTEM: THE INJECTISOME AND MOLECULAR SYRINGE MECHANISM

Type III secretion system is among the most advanced molecular delivery systems that have been developed by bacteria. This system works as an actual syringe capable of transporting protein molecules into the cell cytoplasm. The Type III system involves the assembly of over twenty proteins called the "Hrp" proteins. This system makes up the needle complex, which acts like a needle extending from the bacterial surface and can be inserted into the plant cell membrane once there is physical contact between the two membranes. This needle will create a protein transport channel to allow the injection of proteins into the cytoplasm. Another extensively researched organism with T3SS that secretes various kinds of effectors in plant cells is *Pseudomonas syringae*, which has Hop proteins among those it injects into plant cells, thus blocking host signal transduction pathways. To overwhelm the host immune system, this organism utilizes a sophisticated strategy of secreting 20-30 effectors in one time. *Xanthomonas* utilizes T3SS in order to secrete XopX effectors and similar effectors in order to block plant apoptosis and proliferation of the pathogen. This is quite a different approach from enzymatic degradation, which involves host signaling pathways at the molecular level. The T3SS is

considered the major virulence factor that determines pathogenic specificity in these organisms, as complete deletion of T3SS genes leads to loss of pathogenicity in strains previously pathogenic. *Ralstonia solanacearum*, the causal agent of bacterial wilt diseases, is another organism that utilises T3SS in order to introduce about 70 effector proteins into plant cells, leading to complex alterations of host signaling pathways for its multiplication and vascular spread.

7. TYPE IV AND TYPE V SECRETION SYSTEMS: SPECIALIZED PATHOGENIC STRATEGIES

Type IV secretion system is the only bacterial secretion system that can secrete DNA to facilitate horizontal gene transfer and DNA-protein complex translocation. T4SS is used by the pathogen *Agrobacterium tumefaciens* to perform transformation in plants. *A. tumefaciens* uses the secretion system to move T-DNA (transfer DNA) from its Ti (tumour-inducing) plasmid into the nuclei of the plant cells. Crown gall disease occurs as a result of a transformation of the plant development process through the introduction of bacterial genes into the genome of the plant, leading to the formation of tumours in the form of excessive growth in the plants. Type V secretion system, or the autotransporter pathway utilizes a smart secretory mechanism where the secreted protein forms the translocating channel through the membrane. This type of secretory system comprises a protein with a β -barrel domain in the outer membrane. T5SS proteins secrete themselves through their own pathway. Adhesin proteins produced by *Xylella fastidiosa* and some species of *Xanthomonas* are responsible for the production of biofilm by acting as attachment factors for the plant tissues and biofilm matrix organization.

8. TYPE VI SECRETION SYSTEM: EMERGING PHAGE-LIKE EFFECTOR DELIVERY

Recent studies of Type VI secretion systems (T6SS) demonstrate that they constitute a new kind of pathogenicity system, characterized by a phage-tail-like structure. T6SS comprises contractile protein complexes similar to bacteriophage tails and contains proteins such as Hcp (hemolysin co-regulated protein) and VgrG (valine-glycine repeat protein). After activation, the molecular "spears" contract rapidly and inject effector proteins into the target cells. *Pseudomonas aeruginosa* uses the T6SS as a competitive weapon against other bacteria by injecting antimicrobial factors into competing bacteria. Bacteria such as *Xanthomonas* and *Pectobacterium* use T6SS, which plays a role in their virulence and in modulating plant-microbe and microbe-microbe interactions. Participation of T6SS in microbiome structuring that defines which bacteria

will survive and which ones will not in plant tissue is one of the latest discoveries related to this topic.

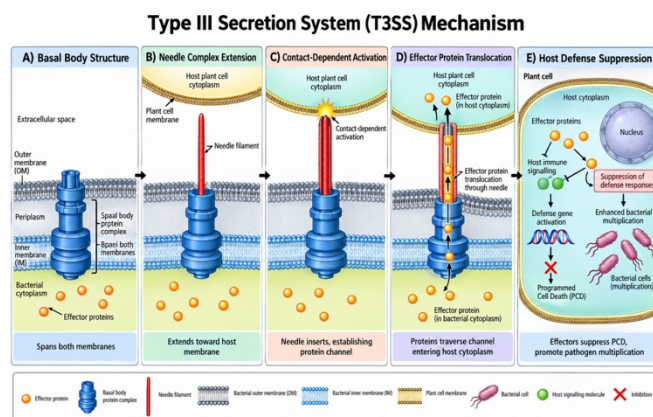


Figure 2. Type III Secretion System Mechanism of Effector Protein Injection

Molecular description of the pathogenic process by T3SS. (A) The basal body spanning both the bacterial inner and outer membranes; (B) The needle structure pointing toward the host cell membrane; (C) Upon activation via contact, the needle penetrates the host cell membrane to form a protein transport channel; (D) Effectors pass through the needle structure into the host cell cytoplasm; (E) Injected effectors inhibit the host cell defense signaling, blocking apoptosis and multiplying the pathogens.

9. CLASSICAL SECRETORY PATHWAYS: FOUNDATIONAL MECHANISMS FOR GRAM-POSITIVE AND GRAM-NEGATIVE BACTERIA

Gram-positive as well as Gram-negative bacteria use the classical Sec (secretory) pathway as their main mode of secreting proteins via the cytoplasmic membrane. This evolutionarily conserved pathway identifies N-terminal signal peptides associated with the newly synthesized proteins and channels them towards the SecYEG translocase pore. It facilitates the transport of unfolded proteins using energy from ATP through the motor protein SecA. The Tat (twin-arginine translocation) pathway offers an alternate option for protein secretion, which is specifically evolved to facilitate the secretion of fully folded proteins that have their redox cofactors intact. This pathway identifies the signal peptides carrying the twin-arginine motif and uses the proton-motive force without ATP hydrolysis to transport the folded substrate across the membrane. Such an ability of the Tat pathway allows for the secretion of complex enzymes like nitrate reductase, hydrogenases, and other metalloproteins.

In Gram-positive bacteria, which have cytoplasmic membrane and outer cell wall layers only, Sec and Tat systems are adequate for secretion. Gram-negative bacteria also utilize these classical systems as basic systems, where many parts of the T2SS, T3SS, and other secretion systems are transported using Sec system transporters. Such dependence on the architecture shows that the development of secretion systems is based on the existing transport systems.

10. Implications for Disease Management and Future Perspectives

Understanding of secretion mechanisms by bacteria is leading to new possibilities for designing new therapies which will utilize the pathogen's dependency on these machineries. Some of the strategies include:

10.1 Secretion Inhibitors: These can potentially make good antimicrobial agents as they can interfere with the secretion process. Preliminary investigations into inhibitors of Hrp needle complex formation in T3SS pathogens hold great promise as novel disease management strategies.

10.2 Effector-Mediated Plant Immunity: Some bacterial effectors are recognized by plant resistance proteins, which activate the plant's immune system. Natural diversity in effector recognition systems is being exploited to breed for disease resistance.

10.3 Engineering Bacteria without Secretion Machinery: Innovative disease management strategies can be created using synthetic biology technologies and CRISPR-based gene editing of essential secretion machinery genes.

11. CONCLUSION

Bacterial secretion systems can be understood to be molecular secretion machineries that allow pathogenic bacteria to infect their host plants. Be it the direct membrane transfer mechanism of Type I secretion systems, the needle injection of cytoplasm of Type III secretion systems or the ability of Type IV secretion systems to transfer DNA, all of these have evolved into highly efficient virulence factors. Plant pathogenic bacteria such as *Pseudomonas*, *Ralstonia*, *Xanthomonas*, and *Erwinia* bacteria utilize more than one type of secretion system in tandem with each other to counteract both the physical structures of plants as well as signal networks inside plants. It is evident from the above discussion that the virulence strategies of plant pathogenic bacteria have been evolving into more complex and redundant structures over time. As the knowledge base about the architecture and working mechanisms of bacterial secretion systems

expands, opportunities for designing new disease management strategies are emerging. Combining these with new methods in plant breeding, synthetic biology, and chemical biology would revolutionize disease control practices in future agriculture.

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