academicJournals

Vol. 8(30), pp. 2809-2815, 23 July, 2014
DOI: 10.5897/AJMR2014.6935
Article Number: E4E1E1146272
ISSN 1996-0808

http://www.academicjournals.org/AJMR

African Journal of Microbiology Research

*Review*

# Virulence strategies of phytopathogenic bacteria and their role in plant disease pathogenesis

**Setti Benali[1]*, Bencheikh Mohamed[2] and Henni Jamel Eddine[3]**

[1]Laboratoire de Phytopathologie, Institut des Sciences Agronomiques, Université de Chlef, Algérie.
[2]Centre universitaire de Khemis Meliana, Ain Defla.44000, Algérie.
[3]Laboratoire de phytopathologie, Faculté des Sciences Université Es Senia, Oran, Algérie.

Received 1 June, 2014; Accepted 7 July, 2014

**Phytopathogenic bacteria have evolved several virulence strategies to face hostile environment of the host plant. In this article, we reviewed the recent progress in research on characterization of the virulence factors including secretion system with their protein effectors, toxins production, extracellular polysaccharides, growth regulators, cell wall degrading enzymes, biofilm formation, siderophores and their role in the plant infection and symptom development focusing particularly on a group of bacteria such as *Erwinia amylovora*, *Agrobacterium tumefaciens*, *Pseudomonas syringae*, *Ralstonia solanacearum* and *Xanthomonas compestris* that cause different plant diseases including wilts, spots, blights and cankers. The elucidation of each step in pathogenesis may constitute a key step in any design of new molecules for targeting plant pathogenic bacteria for plant disease control.**

**Key words:** Virulence factors, plant disease, phytopathogenic bacteria, phytotoxins, secretion systems, siderophores.

## INTRODUCTION

Most phytopathogens must evolve numerous strategies to survive in different environmental conditions to invade and colonize their hosts known as virulence factors. These factors have the ability to modulate the physiological and biochemical mechanisms to enhance the spread of the pathogen, as well as to facilitate the release of nutrients and water from host cells (Toth et al., 2003).

The plant bacterial pathogens, involve many virulence factors that are secreted in the extracellular environment of the host cells. The most studied factors are: (1) adherence to the host cells, with surface adhesins, (2) production of the degradative enzymes that destroy the plant cells walls, (3) toxins that are in the apoplastic cell, (4) other complex molecules are also deployed including the exopolysaccharide (EPS) and those modulating the

*Corresponding author. E-mail: setiben@yahoo.fr.

plant hormone production. The major intensive studies in the field of plant bacteria interactions are the characterization of the pathogen virulence factors and their main roles in the pathogenecity and the specificity of the host. The elucidation of such aspect may lead to the planning and establishment of new strategy in the plant disease control. In the following section, we overviewed the recent development of the function and mechanism in the plant bacterial pathogens.

## SECRETION SYSTEM

Plant pathogenic bacteria have evolved numerous sophisticated strategies for selective transport of proteins and nucleoproteins involved in the virulence across cell membranes in both the apoplastic environment and the cytoplasmic of the plant cells. Currently, six major classes of systems implicated in the virulence have been identified and described in plant pathogenic bacteria named from type I to type VI or T1SS to T6SS. The translocation mechanism of effector proteins from the bacterial cytosol to the external bacterial cell is known as secretion (Alfano et al., 2000).

In plant pathogenic Gram-negative bacteria, two major system are described. The single step process, in which secretion proteins are exported across the inner and the outer membrane without any periplasmic step, however, the two steps process namely the Sec and the Tat secretion system are first exported in the periplasmic and then transported across the external membrane to the exterior of bacteria cell. In the following section, we summarized the general features of the six identified secretion system known in the phytoopathogenic Gram-negative bacteria (Alfano et al., 2000; Preston et al., 2001).

### T1SS secretion sytem

In phytopathogenic Gram-negative bacteria, the type I secretion system also known as the ATP binding cassette (ABC) transporters is involved in the export of various molecules from the cytosol to the external environment without any periplasmic step (Delepelaire et al., 2004). The type I secretion system consists of three distinct proteins that compose a continuous chanel (Ian et al., 2006). The inner membrane ATP binding cassette (ABC) proteins transporters is a specific outer membrane known as outer membrane protein (OMP) and the so called membrane fusion protein (MFP) which is connected to the inner membrane and spans the periplasmic space and extends to the outer membrane(Ian et al., 2006). Many proteins of great importance in pathogenesis are transferred by the ABC secretion system in plant pathogenic bacteria including proteases, lipases or performing toxins. The T1SS is required for numerous plant pathogenic Gram-negative bacteria including both the *Erwinia amylovora* and *Erwinia chrysanthemi* (Ian et al., 2006; Liu et al., 2008).

### T2SS secretion system

In Gram-negative bacteria, the T2SS secretion system known as the sec dependant system translocate folded proteins across the inner membrane either by sec pathway or Tat pathway to the periplasm and then the extracellular environment. The plant pathogenic bacteria, uses such a system to export hydrolytic enzymes involved in degrading different plant substrates including cellulases, xylanases, amylases and proteases. Several plant pathogenic bacteria include *Pseudomonas fluorescens*, *Erwinia carotovora* pv *atroseptica*, *Xanthomonas compestris* pv *compestris* and *X. oryzae* pv *oryzae* (Peabody et al., 2003).

### T3SS secretion system

Several plant bacterial pathogens have evolved a strategy of delivering an array of effectors and toxins proteins directly into the cytoplasm of host cells known as the type III secretion systems (Preston et al., 2001; Lindeberg et al. 2012). Theses virulence determinants have the capacity to modulate the physiological functions (Staskawicz et al., 2001; Buttner and Bonas, 2003). The type III secretion apparatus is composed of more than of 20 proteins consisting of basal body spanning both the inner and the outer membrane of the bacterial cells, and an extracellular needle with a tip complex extending into the host cell (Staskawicz et al., 2001). The TTSS in phytopathogenic bacteria is encoded by hypersensitive response and pathogenecity (hrp) gene involved in the transfer of Avr proteins in the host cell inducing both either pathogenecity on sensitive host or hypersensitive reaction on resistant host. The plant pathogens that use the TTSS system include *Xanthomonas* spp., *Erwinia* spp., *Pseudomonas syringae* and *Ralstonia solanacearum* (Birch, 2001; Noel et al., 2002; Angot et al., 2006).

### T4SS secretion system

The type IV secretion system (T4SS) is present in both the Gram-negative and positive plant pathogenic bacteria (Wallden et al., 2010). This tranlocation system is an important system that deploy the sec gene to transport

the pathogenecity factors from the inner bacterial cell into the extracellular environment or directly into the plant host cell (Judd et al., 2005). The type IV secretion system is involved in the translocation into the plant cell of either the single stranded DNA (ssDNA), the multi subunit toxins or the monomeric proteins including the permeases. This secretion system is related to a conjugation machines. Among the most representative phytopathogenic bacteria that uses the T4SS secretion system is *Agrobacterium tumefaciens* that target the oncogenic DNA-protein complex in plant cell (Zupan et al., 2000; Juhas et al., 2008; Wallden et al., 2010).

### T5SS secretion system

The type V secretion system (T5SS) is widely present among the Gram-negative bacteria (Tseng et al., 2009). This translocation system is considered as one of the simplest secretion pathway (Desvaux, 2004; Tseng et al., 2009). The T5SS translocation system is dedicated to transfer a single specific polypeptide known as the passenger domain in two step process (Moreira et al., 2004). The first step is mediated by a sec translocator across the inner membrane. The second step concerns the own transportation of the passenger through the outer membrane by forming a protected module called a β barrel (Van Sluys et al., 2002). During the translocation of passenger domain, the signal sequence can either remain on the bacterial surface or cleave and then released in the extracellular milieu. The type V secretion system can exist in two subtypes which are the autotransporters (AT) system (Type Va) and the TPS nown as AT-2. In Gram-negative bacteria, the virulence factors associated with T5SS passenger are numerous including biofilm formation, adhesins, toxins, enzymes production and cytotoxic activity (Leo at al., 2012; Jacob-Dubuisson, 2013). Among the plant pathogenic Gram-negative bacteria that involve the T5SS secretion system as pathogenicity determinant include *Xylella factidiosa,* the causative agent of Pierce's disease (Igo et al., 2007), the Xanthomonads (Van Sluys et al., 2002; Moreira et al., 2004) and *E. chrysanthemi* (Tseng et al., 2009).

### T6SS secretion system

The type VI secretion system (T6SS) has been recently discovered as new mechanism for effectors transportation across the cell membrane in the Gram-negative bacteria (Bingle et al., 2008, Filloux et al., 2008; Shrivastava and Mande, 2008; Pukatzki et al., 2010). The structure of the T6SS secretion system presents a significant similarity with the bacteriophage tails which inject their effector protein proteins either directly into the host cell or in the extracellular milieu (Tseng et al., 2009; Pukazki et al., 2010). The T6SS secretion system is involved in the translocation of numerous pathogenicity determinants including the biofilm formation, the quorum sensing and antibacterial toxins. This secretion mechanism has been identified in many Gram-negative bacteria including *Agrobacterium tumificiens*, *Pectobacterium atrosepticum* and *Pseudomonas syringae* (Wu et al., 2008; Records and Gross, 2010) and *Xanthomonas oryzae* (Fillouw et al., 2008).

## PECTIN DEGRADING ENZYMES

Pectin substrate is a complex polysaccharide presents in all plants in the middle lamella of primary cell wall consisting mainly of galacturonic acid residues linked with an α(1-4) glucosidic bond (Pedrolli et al., 2009; Kothari and Baig, 2013). The acid groups are largely esterified with methyl groups. Plant pathogenic bacteria are known to produce an array of inducible extracellular enzymes that degrade plant cell wall constituents (Collmer and Keen, 1986). These enzymes are thought to play a key role as virulence factors. The most enzymes in bacteria plant pathogen and fungi are those degrading the pectin substances which are also the widely studied as determinants (Collmer et al., 2002). Among the widely pectic enzymes in phytopathogenic bacteria are two important classes namely the pectate lyases (PL) and polygalacturonases (PG) (Collmer and Keen, 1986; Saile et al., 1997). The plant pathogens that secrete complexes of pectic enzymes such as the pectate lyases (PL) (Boch et al., 2002; Collmer et al., 2002) and polygalacturonases (PG) includes the soft rot Erwinias namely *E. carotovora* and *E. chrysanthemi* (Barras et al., 1994; Carpita and McCann, 2000; Collmer et al., 2002).

## SIDEROPHORES

Iron is an essential element for nearly all microorganisms including the plant pathogenic bacteria as it participates in numerous process such as redox reactions, oxygen binding and as cofactors for vital enzymes (Buyer and Leong, 1986). To maintain the availability of the free iron at acceptable concentration to limits the growth of invading bacterial pathogen, the host uses two major proteins for the transport and storage of free iron including the transferins and ferritins (Dave and Dube, 2000; Gull and Hafeez, 2012). Many plant pathogenic bacteria secrete molecular weight for ferric ion ($Fe^{3+}$) chelate and transfer agent known as siderophores from the host then pumped in the bacteria cytosol by specific

membrane receptors (Leong and Neilands, 1981, Williams and Griffiths, 1992). Siderophores have been shown to play a major role as virulence factors for numerous plant pathogenic bacteria in plant disease. Among the compounds secreted include chrysobactin which is a catechol by *E. chrysanthemi* and *E. carotovora* (Perswerk et al., 1989; Alfano and Collmer, 2004) and the hydroxamate which is a siderophore produced by *Agrobacterium tumefaciens* (Leong and Neilands, 1981). Another iron transportation system mediated by specific proteins is known as NRAMP activated by infected plant particularly in response to biotic stress or iron limitation in plant host. The NRAMP are now known to be involved in innate immunity and to be the basic resistance for plant towards the pathogens( Expert et al., 2012; Dellagi et al., 2009).

## ANTIMICROBIAL COMPOUNDS DETOXIFICATION

For the defense mechanisms, most plants produce antimicrobial compounds as secondary metabolites in response to pathogen infection (Glazebrook et al., 1997). Phytoalexins are among these antimicrobial substances which are considered as molecules at sufficient concentration that limit and reduce the growth and multiplication of pathogenic microorganisms (Hammond-Kosack and Jones, 1996). Among the major studied and illustrated compounds are pisatins in peas (VanEtten et al., 1975; Van Etten et al., 1989), saponins in oats, isoflavonoids in legumes and terpenoids in Solanaceae (Turbek et al., 1992). On the other hand, different mechanisms were described particularly in fungi which counter these antimicrobial substances. The pisatin are detoxified by cytochrome CP 450 monoxygenase (Matthews and Van Etten, 1983). Similarly, *Fusarium oxysporum f.sp. Lycopersicum* produce an inducible extracellular enzyme known as tomatinase which detoxifies the alpha tomatine. Furthermore, most Xanthomonads detoxify reactives oxygen and superoxyde species using catalases (Qian et al., 2005). Recently, two inducibles enzymes were secreted by *Pseudomonas syringae*are involved in the isothiocyanates detoxification (Fan et al., 2011).

## TOXINS (PATHOTOXINS)

Plant pathogenic bacteria are known to produce a wide range of both specific and nonspecific host phytotoxins. Some are polypeptids, glycoproteins others are secondary metabolites that are required as virulence factors in plant disease (Alfano and Collmer, 2004). These toxins acts by using diverse mechanisms from modulating and suppressing plant defense response to alteration and inhibition of normal host cellular metabolic process (Thomas et al., 1983). These toxins act also directly on the expression and development of disease symptoms. Among the most well studied pathotoxins known also as phytotoxins include syringomycins, syringopeptins, tabtoxins, phaseolotoxins and coranotine described particularly in *P. syringae* pathovars(Thomas et al., 1983).

### Syringomicins and syringopeptins

Both syringomycins and syringopeptins are a group of polar cyclic peptidide known as lepodepsipeptides toxins which are secreted by several pathovars of *P. syringae* (Lu et al., 2005). These toxins act by disrupting the host cell membrane forming small pores leading to the electrolyte leakage from plant cell cytoplasm inducing necrosis of plant tissue of affected plant (Blender et al., 1999).

### Coronatine

Plant pathogenic coronatine is produced by several pathovars of *P. syringae* and contribute as virulence factor. Coronatine consists of two major polyetide components, the coronafacic acid and coronamic acid molecules. Coronatine share similarity in structure with jasmonic acid-isoleucine(JA-Ile) and hence mimic them (Brooks et al., 2005; Katsir et al., 2008). Coronatine plays a key role in early stage of infection by inhibition of the stomatal immune defense leading to the entry of the pathogen. This toxin counteract the pathogen associated molecular patterns (PAMPs) induced stomatal closure in both *P. syringae* and *X. compestris* (Hutchison and Gross, 1997; Gommez-Gomez and Boller, 2002). In fact, PAMPs consists of conserved components motifs that include flagellin and lipolysaccharide (LPS). These molecular patterns are recognized by plant pathogen recognition receptors (PRRs). These perception of PAMPs activates the basal defenses mechanisms in early stages of interaction of plant pathogen interaction (Bittel and Robatzek, 2007; Melotto et al., 2008; Nurnberger and Kemmerling, 2009). On the other hand, these pathotoxin also contribute to expression of other diseases including the chlorosis symptoms, hypertrophy and lesion formation (Sekai et al., 1979; Brooks et al., 2005). Another well studied class of siderophores, are those synthetized by fluorescent pseudomonads. Pyoverdine play a key role in controlling iron availability in the rhizosphere (Visca et al., 2002; Expert et al., 2012). On the other hand, the pyoverdine was recently identified as virulence factors in *P. syringae* pv.tabaci (Tagushi et al., 2010).

### Phaseolotoxins

Phaseolotoxins are synthetized by different pathovars of

*Pseudomonas syringae* including the pathovars phaseolicola and actinidia. The phaseolotoxin is a tripeptide which is hydrolyzed to produce an octicidine metabolite that is an irreversible inhibitor of ornithine carbonoyl transferase (OCTase) (Arrebola et al., 2003; Melotto and Kunkel, 2013). The OCTase enzyme is considered to play a major role in the urea cycle of the plant (Arrebola et al., 2003).

The tabotoxinine beta lactam (TBL), the active form of the tabotoxine is produced in the host plant after hydrolosis with an aminopeptidase (Moore et al., 1984; Arrebola et al., 2007). The TBL pathotoxin plays a key role as an inhibitor of the glutamic synthetase (Thomas et al., 1983). Both the tabtoxines and phaseolotoxins contribute to the virulence of the *P. syringae* by inhibiting the host response defense at early stage and by inhibiting the photosynthesis process leading to severe chlorosis of the affected plant tissues (Arrebola et al., 2007).

## ADHESINS AND EXTRACELLULAR POLYSACCHARIDES

Adhesins are considered as biomolecules such as proteins and glycoproteins that mediate the binding of the bacteria to the host cell (Katzen et al., 1996). The adherence is the first step interaction between the pathogen and the plant host which lead to the attachment and colonization of foliage or root tissues of the host plant (Kao et al., 1992; Alfano and Collmer, 1996). The plant pathogenic bacteria utilize several types of adhesins including a proteinous fimbrial or non fimbrial adhesions. Another group of adhesins which play key role in numerous plant pathogen interaction are the exopolysaccharides (EPS) (Kim et al., 2003; Melotto and Kunkel, 2013). The EPS are carbohydrate compounds secreted and maintained tightly associated with the bacterial capsule or released around the bacterial matrix. The importance of adhesins as virulence factors has been studies in numerous plant pathogens. Hence, *X. compestris* produce a major exopolysaccharide known as Xanthan gum implicated in infection (Denny, 1995; Melotto and Kunkel, 2013). The EPS amylovorin is another example of adhesins produced by *E. amylovora*, the causal agent of fire blight. *P. syringae*, the causal agent of several plant diseases produces different EPS such as alginate, levan (Denny, 1995). Proteinous fimbrial adhesins are also implicated in the infection caused by *P. syringae* (Yu et al., 1999).

## QUORUM SENSING AND BIOFILM PRODUCTION

Quorum sensing is a bacterial communication mechanism that regulates the density of microbial population using the gene expression in response to the environmental and chemical sensing system (Kanda et al., 2011; Melotto and Kunkel, 2013). The signal molecules known as autoinducers that are detected by different bound receptors of bacterial cells are produced in coordinate manner at a specific bacterial stage such as disease physiological function including epiphytic growth, competition or colonization and virulence stage (von Bodman et al., 2003; Kanda et al., 2011). Quorum-sensing signal N-acyl homoserine lactones are known to regulate numerous virulence factors including enzymes production and exopolysaccharides in many plant pathogenic bacteria (Teplitski et al., 2000). Among the quorum-sensing regulator detected in *P. syringae* PsrA, is Pel regulator in *E. chrysanthemi.* However, a series of reglators namely MqsR, QseBC and exporter TqsA, could be present in *E. amylovora* (Hugouvieux-Cotte-Pattat et al., 1992).

Biofilm is a complex multilayer cellular structure attached to an inanimate surface or tissues and embedded within an exopolysaccharide material (Welch et al., 2000; Dow et al., 2003). Biofilm provides a protection for bacterial cell from a wide range of hostile and extreme environmental conditions including deshydratation, extreme pH and UV radiation (Welch et al., 2000; Melotto and Kunkel, 2013).

Biofilm also shield bacteria cell from host immune response and antimicrobials compounds (Dow et al., 2003). Several plant pathogenic bacteria have been considered as biofilm producer as virulence factors including *X. compestris* (Dow et al., 2003) and *P. syringae* (Keith et al., 2003).

## CONCLUSION

Based on several advances in literature on bacterial disease, it is clear that plant bacteria expresses virulence factors in each specific stage of pathogenesis. The virulence of plant pathogens is a multifactorial phenomenon which involves host-pathogen interactions that must be largely explored. In this review, we summarized the major bacterial virulence determinants that are required for establishing infection and disease development. On the other hand, an efficient strategy for bacterial disease control needs further studies of the virulence factors at the molecular levels in order to know their contribution in the plant pathogen interaction.

## Conflict of Interest

The authors have not declared any conflict of interest.

## REFERENCES

Alfano JR, Charkowski AO, Deng WL, Badel JL, Petnicki-Ocwieja T, van Dijk K, Collmer A (2000). The Pseudomonas syringae Hrp pathogenicity

island has a tripartite mosaic structure composed of a cluster of type III secretion genes bounded by exchangeable effector and conserved effector loci that contribute to parasitic fitness and pathogenicity in plants. Proc. Natl. Acad. USA 97:4856-4861

Alfano JR, Collmer A (1996). Bacterial pathogens in plants: life up against the wall. Plant Cell 8:1683-1698.

Alfano JR, Collmer A (2004). Type III secretion system effector proteins: double agents in bacterial disease and plant defense. Annu. Rev. Phyopathol. 42:385-414.

Angot A, Peeters N, Lechner E, Vailleau F, Baud C, Gentzbittel L, Sartorel E, Genschik P, Boucher C, Genin S (2006). Ralstonia solanacearum requires F-box-like domain-containing type III effectors to promote disease on several host plants. Proc. Natl. Acad. Sci. USA 103:14620-14625.

Arrebola E, Cazorla FM, Dura´n VE, Rivera E, Olea F, Codina JC, Pe´rez-Garci´a A,de Vicente A (2003). Mangotoxin: a novel antimetabolite toxin produced by Pseudomonas syringae inhibiting ornithine/arginine biosynthesis. Physiol. Mol. Plant Pathol. 63:117-127.

Arrebola E, Cazorla FM, Romero D, Pe´rez-Garcı´a A, de Vicente A (2007). A nonribosomal peptide synthetase gene (mgoA) of Pseudomonas syringae pv. syringae is involved in mangotoxin biosynthesis and is required for full virulence. Mol. Plant Microbe Interact. 20:500-509.

Barras F, Gijsegem FV, Chatterjee AK (1994). Extracellular enzymes and pathogenesis of soft-rot Erwinia. Annu. Rev. Phytopathol. 32:201-234.

Bingle LE, Bailey CM, Pallen MJ (2008). Type VI secretion: a beginner's guide. Curr. Opin. Microbiol. 11(1):3-8.

Birch RG (2001). Xanthomonas albilineans and the antipathogenesis approach to disease control. Mol Plant Pathol 2:1-11.

Brooks DM, Bender CL, Kunkel BN (2005). The Pseudomonas syringae phytotoxin coronatine is required to overcome salicylic acid-mediated defenses in Arabidopsis thaliana. Mol. Plant Pathol. 6:629-639.

Buttner D, Bonas U (2003). Port of entry the type III secretion translocon. Trends Microbiol. 10:186-192.

Buyer JS, Leong J (1986). Iron transport mediated antagonism between plant growth promoting and plant deleterious Pseudomonas strains. J. Biol. Chem. 261:791-794.

Collmer A, Keen NT (1986). The Role of Pectic Enzymes in Plant Pathogenesis. Ann. Rev. Phytopathol. 24: 383-409.

Collmer A, Lindeberg M, Petnicki-Ocwieja T, Schneider DJ, Alfano R (2002). Genomic mining type III secretion system effectors in Pseudomonas syringae yields new picks for all TTSS prospectors. Trends Microbiol. 10:462-469.

Dave BP, Dube H (2000). Detection and chemical characterisation of siderophores of rhizobacterial fluorescent pseudomonads. Ind. Phytopathol. 53:97-98.

Delepelaire P (2004). Type I secretion in gram-negative bacteria. Biochim. Biophys. Acta 1694:149-161.

Dellagi A, Segond D, Rigault M, Fagard M, Simon C, Saindrenan P, Expert D (2009) Microbial siderophores exert a subtle role on Arabidopsis during infection by manipulating the immune response and the iron status. Plant Physiol. 150:1687-1696.

Denny TP (1995). Involvement of bacterial polysaccharides in plant pathogenesis. Ann. Rev. Phytopathol. 33:173-197.

Desvaux M, Parham NJ, Henderson IR (2004). Type V protein secretion: simplicity gone awry? Curr. Issues Mol. Biol. 6:111-124.

Dow JM, Crossman L, Findlay K, He YQ, Feng JX, Tang JL (2003). Biofilm dispersal in Xanthomonas campestris is controlled by cell-cell signaling and is required for full virulence to plants. Proc. Natl. Acad. Sci. USA 100:10995-11000.

Expert D, Franza T, Dellagi A (2012). Molecular Aspects of Iron Metabolism in Pathogenic and Symbiotic Plant-Microbe Associations, SpringerBriefs in Biometals, DOI: 10.1007c/978-94-007-5267-2_2.

Fan J, Hill L, Crooks C, Doerner P, Lamb C (2009). Abscisic acid has a key role in modulating diverse plant-pathogen interactions. Plant Physiol. 150:1750-1761.

Filloux A, Hachani A, Bleves S (2008). The bacterial type VI secretion machine: yet another player for protein transport across membranes. Microbiology 154(Pt 6):1570-1583.

Glazebrook J, Rogers EE, Ausubel FM (1997). Use of Arabidopsis for genetic dissection of plant defense responses. Annu. Rev. Genet. 31:547-569.

Gull M, Hafeez FY (2012). Characterization of siderophore producing bacterial strain Pseudomonas fluorescens Mst 8.2 as plant growth promoting and biocontrol agent in wheat. Afr. J. Microbiol. Res. 6(33):6308-6318.

Hammond-Kosack K, Jones JDG (2000). Responses to plant pathogens. In: Buchanan BB, Gruissem W, Jones RL (eds) Biochemistry and molecular biology of plants. American Society of Plant Physiologists, Rockville. pp. 1102-1156.

Hugouvieux-Cotte-Pattat N, Dominguez H, Robert-Baudouy J (1992) Environmental conditions affect transcription of the pectinase genes of Erwinia chrysanthemi 3937. J. Bacteriol. 174: 7807-7818

Hutchison ML, Gross DC (1997). Lipopeptide phytotoxins produced by Pseudomonas syringae pv. Syringae: Comparison of the biosurfactant and ion channelforming activities of syringopeptin and syringomycin. Molec. Plant-Microbe Interact. 10:347-354.

Ian K. T, LP, Birch, PRJ (2006). Comparative Genomics Reveals What Makes An Enterobacterial Plant Pathogen. Ann. Rev Phytopathol. 44:305-336.

Igo MM, Matsumoto A, Kirkpatrick B (2007). The role of type V secretion autotransporters in the virulence of Xylella fastidiosa, Pierce's disease research symposium. California Department of Food and Agriculture, San Diego, CA. pp. 140-143.

Judd PK, Kumar RB, Das A (2005). The type IV secretion apparatus protein VirB6 of Agrobacterium tumefaciens localizes to a cell pole. Mol. Microbiol. 55:115-124.

Juhas M, Crook DW, Hood DW (2008). Type IV secretion systems: tools of bacterial horizontal gene transfer and virulence. Cell. Microbiol. 10:2377-2386.

Kao CC, Barlow E, Sequeira L (1992). Extracellular polysaccharide is required for wild-type virulence of Pseudomonas solanacearum. J Bacteriol 174:1068-1071.

Katzen F, Becker A, Zorreguieta A, Pühler A, Ielpi L (1996). Promoter analysis of the Xanthomonas campestris pv. campestris gum operon directing biosynthesis of the xanthan polysaccharide. J. Bacteriol. 178:4313-4318.

Keith RC, Keith LM, Hernandez-Guzman G, Uppalapati SR, Bender CL (2003). Alginate gene expression by Pseudomonas syringae pv. tomato DC3000 in host and non-host plants. Microbiology 149:1127-1138.

Kim JG, Park BK, Yoo CH, Jeon E, Oh J, Hwang I (2003). Characterization of the Xanthomonas axonopodis pv. glycines Hrp pathogenicity island. J. Bacteriol. 185:3155-3166.

Kothari MN, Baig MV (2013). Production and characterization of extracellular polygalacturonase by Erwinia carotovora MTCC 1428. Int. J. Adv. Biotechnol. Res. 4(1):118-122.

Lindeberg M, Cunnac S, Collmer A (2012). Pseudomonas syringae type III effector repertoires: last words in endless arguments. Trends Microbiol. 20:199-208.

Liu H, Coulthurst SJ, Pritchard L, Hedley PE, Ravensdale M, et al. (2008). Quorum Sensing Coordinates Brute Force and Stealth Modes of Infection in the Plant Pathogen Pectobacterium atrosepticum. PLoS Pathog. 4(6):e1000093.

Lu SE, Wang N, Wang J, Chen ZJ, Gross DC (2005). Oligonucleotide microarray analysis of the Sal A regulon controlling phytotoxin production by Pseudomonas syringae pv. syringae. Mol. Plant Microbe Interact. 18:324-333.

Matthews, DE, Van Etten HD (1983). Detoxification of the phytoalexin pisatin by a fungal cytochrome P-450. Arch. Biochem. Biophys. 224:494-505.

Melotto M, Underwood W, He SY (2008). Role of stomata in plant innate immunity and foliar bacterial diseases. Annu Rev Phytopathol 46:101-122.

Melotto M, Kunkel BN (2013). Virulence Strategies of Plant Pathogenic Bacteria in E. Rosenberg et al. (eds.), The Prokaryotes - Prokaryotic Physiology and Biochemistry, DOI 10.1007/978-3-642-30141-4_62.

Moore RE, Niemczura WP, Kwok OCH, Patil SS (1984). Inhibitors of ornithine carbamoyltransferase from Pseudomonas syringae pv. phaseolicola. Tetrahedr. Lett. 25:3931-3934.

Moreira LM, de Souza RF, Almeida Jr NF, Setubal JC, Oliveira JC, Furlan LR, Ferro JA, da Silva AC (2004). Comparative genomics analyses of citrus-associated bacteria. Annu. Rev. Phytopathol. 42:163-184.

Noel L, Thieme F, Nennstiel D, Bonas U (2002). Two novel type III-secreted proteins of Xanthomonas campestris pv. vesicatoria are encoded within the hrp pathogenicity island. J. Bacteriol. 184:1340-1348.

Peabody CR, Chung YJ, Yen MR, Vidal-Ingigliardi D, Pugsley AP, Saier MH (2003). Type II protein secretion and its relationship to bacterial type IV pili and archaeal flagella. Microbiology 149:3051-3072.

Pedrolli DB, Monteiro AC, Gomes E, Carmona EC (2009). Pectin and Pectinases: Production, Characterization and Industrial Application of Microbial Pectinolytic Enzymes. Open Biotechnol. J. 3:9-18.

Preston GM, Bertrand N, Rainey PB (2001). Type III secretion in plant growthpromoting Pseudomonas fluorescens SBW25. Mol. Microbiol. 41:999-1014.

Pukatzki S, Sturtevant D, Krastins B, Sarracino D, Nelson WC, Heidelberg JF, Mekalanos JJ (2006). Identification of a conserved bacterial protein secretion system in Vibrio cholerae using the Dictyostelium host model system. Proc. Natl. Acad. Sci. U. S. A 103:1528-1533.

Qian W, Jia Y, Ren SX, He YQ, Feng JX, Lu LF, et al. (2005). Comparative and functional genomic analyses of the pathogenicity of phytopathogen Xanthomonas campestris pv. Campestris. Genome Res. 15:757-67.

Saile E, McGarvey JA, Schell MA, Denny TP (1997). Role of extracellular polysaccharide and endoglucanase in root invasion and colonization of tomato plants by Ralstonia solanacearum. Phytopathol 87:1264-1271.

Shrivastava S, Mande SS (2008). Identification and functional characterization of gene components of Type VI secretion system in bacterial genomes. PLoS ONE, 3(8):e2955.

Staskawicz BJ (2001). Genetics of plant-pathogen interactions specifying plant disease resistance. Plant Physiol. 125:73-76.

Teplitski M, Robinson JB, Bauer WD (2000).Plants Secrete Substances That Mimic Bacterial N-Acyl Homoserine Lactone Signal Activities and Affect Population Density-Dependent Behaviors in Associated Bacteria. Phytopathology (13:6):637-648.

Thomas MD, Langston-Unkefer PJ, Uchytil TF, Durbin RD (1983). Inhibition of glutamine synthetase from pea by tabtoxinine-beta-lactam. Plant Physiol. 71:912-915.

Toth IK, Bell KS, Holeva MC, Birch PRJ (2003). Soft rot erwiniae: from genes to genomes. Mol. Plant Pathol. 4:17-30.

Tseng TT, Tyler BM, Setubal JC (2009). Protein secretion systems in bacterial-host associations, and their description in the Gene Ontology. BMC Microbiology 9(Suppl 1):S2.

Turbek CS, Smith DA, Schardl CL (1992). An extracellular enzyme from Fusarium solani f. sp. phaseoli, which catalyzes hydration of the isoflavonoid phytoalexin phaseollidin. FEMS Microbiol. Lett. 94:187-190.

VanEtten HD, Matthews DE, Matthews, PS (1989). Phytoalexin detoxification: Importance for pathogenicity and practical implications. Ann. Rev. Phytopathol. 27:143-164.

VanEtten HD, Pueppke SK, Kelsey TC (1975). 3,6a-Dihydroxy- 8,9-methylenedioxy pterocarpan as a metabolite of pisatin produced by Fusarium solani f. sp. pisi. Phytochemistry 14:1103-1105.

Von Bodman SB, Bauer WD, Coplin DL (2003). Quorum sensing in plantpathogenic bacteria. Annu. Rev. Phytopathol. 41:455-482

Wallden K, Rivera-Calzada A, Waksman G (2010). Type IV secretion systems: versatility and diversity in function. Cell. Microbiol. 12: 1203-1212.

Welch M, Todd DE, Whitehead NA, McGowan, SJ, Bycroft BW, Salmond GP (2000). N-acyl homoserine lactone binding to the CarR receptor determines quorum-sensing specificity in Erwinia. EMBO J. 19:631-641.

Williams PH, Griffiths E (1992). Bacterial transferrin receptors-structure, function and contribution to virulence. Med. Microbiol. Immunol. 181:301-322.

Wu HY, Chung PC, Shih HW, Wen SR, Lai EM (2008). Secretome analysis uncovers an Hcp-family protein secreted via a type VI secretion system in Agrobacterium tumefaciens. J. Bacteriol. 190(8):2841-2850.

Yu J, Pen˜aloza-Va´zquez A, Chakrabarty AM, Bender CL (1999). Involvement of the exopolysaccharide alginate in the virulence and epiphytic fitness of Pseudomonas syringae pv. syringae. Mol. Microbiol. 33:712-720.

Zupan J, Muth TR, Draper O, Zambryski P (2000). The transfer of DNA from Agrobacterium tumefaciens into plants: a feast of fundamental insights. Plant J. 23:11-28.