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Pathogen Profile Update

Pantoea ananatis: genomic insights into a versatile pathogen

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SUMMARY: *Pantoea ananatis*, a bacterium that is well known for its phytopathogenic characteristics, has been isolated from a myriad of ecological niches and hosts. Infection of agronomic crops, such as maize and rice, can result in substantial economic losses. In the last few years, much of the research performed on *P. ananatis* has been based on the sequencing and analysis of the genomes of strains isolated from different environments and with different lifestyles. In this review, we summarize the advances made in terms of pathogenicity determinants of phytopathogenic strains of *P. ananatis* and how this bacterium is able to adapt and survive in such a wide variety of habitats. The diversity and adaptability of *P. ananatis* can largely be attributed to the plasticity of its genome and the integration of mobile genetic elements on both the chromosome and plasmid. Furthermore, we discuss the recent interest in this species in various biotechnological applications.

Taxonomy: Domain Bacteria; Class Gammaproteobacteria; Family Enterobacteriaceae; genus *Pantoea*; species *ananatis*.

Disease symptoms: *Pantoea ananatis* causes disease on a wide range of plants, and symptoms can range from dieback and stunted growth in *Eucalyptus* seedlings to chlorosis and bulb rotting in onions.

Disease control: Currently, the only methods of control of *P. ananatis* on most plant hosts are the use of resistant clones and cultivars or the eradication of infected plant material. The use of lytic bacteriophages on certain host plants, such as rice, has also achieved a measure of success.

Keywords: biotechnology, genomics, pan-genome, pathogenicity, quorum sensing, type VI secretion system.

INTRODUCTION

Pantoea ananatis is a species of Gram-negative, rod-shaped, aerobic or facultatively anaerobic, yellow-pigmented bacteria belonging to the class Gammaproteobacteria and the family Enterobacteriaceae (Coutinho and Venter, 2009). Initially, it formed part of the *Erwinia herbicola–Enterobacter agglomerans* complex and was assigned to the genus *Pantoea* when it was established in 1989 (Gavini *et al.*, 1989). *Pantoea uredovora*, a pathogen of *Puccinia graminis*, was shown to have a high level of genomic relatedness to *P. ananatis*, and the two species were synonymized (Mergaert *et al.*, 1993).

Pantoea ananatis has a cosmopolitan distribution and has been found right across the globe, from South Africa in the south (Coutinho *et al.*, 2002; Goszczynska *et al.*, 2007; Weller-Stuart *et al.*, 2014) to Russia in the north (Egorova *et al.*, 2015), Mexico in the west (Perez-y-Terron *et al.*, 2009) and Australia in the east (Murrell *et al.*, 2003). In these areas, this bacterium has an exceptional lifestyle, as it is not only associated with plants, but is also frequently isolated from a wide range of environmental sources. As a plant pathogen, it causes severe losses of many agronomic crop and tree species, such as maize (Goszczynska *et al.*, 2007), rice (Watanabe *et al.*, 1996), onion (Gitaitis *et al.*, 2002) and *Eucalyptus* (Coutinho *et al.*, 2002). *Pantoea ananatis* is also frequently isolated from a wide range of plant hosts as an epiphyte or endophyte, where it exists as a commensal without causing any disease symptoms (Coutinho and Venter, 2009). In addition to its association with plants, *P. ananatis* has been found to be associated with numerous insects (Dutta *et al.*, 2016; Gitaitis *et al.*, 2003; Murrell *et al.*, 2003; Watanabe *et al.*, 1996; Wells *et al.*, 2002), as well as humans (De Baere *et al.*, 2004), where it is capable of causing bacteraemia. As a saprophyte, it has been isolated from a plethora of different environments, ranging from soil and freshwater to aviation fuel tanks (Gasser *et al.*, 2012; Pileggi *et al.*, 2012; Rauch *et al.*, 2006).

Given the ubiquitous nature of *P. ananatis* and its significance as an agronomic phytopathogen with potential clinical relevance, it has been well represented in the genome sequencing era, with a number of plant-pathogenic, plant growth-promoting and environmental isolates being sequenced in the last decade. These genome sequences and comparative genomic analyses of the sequenced genomes with one another and with those of other well-characterized species provide a primer to unravel some of the enigmas of this species, including how it causes disease on such a wide range of plant hosts, how it can spread between hosts and what enables this bacterium to occupy such a diverse range of ecological niches.

Previously, we have reviewed some of the key concepts regarding the taxonomic background, microbiological properties, disease symptoms, control and epidemiology of *P. ananatis*

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(Coutinho and Venter, 2009). Furthermore, we have highlighted some of the gaps in our knowledge on this emerging phytopathogen, including the pathogenicity and host range determinants, as well as the ability to adapt and survive in a wide range of habitats (Coutinho and Venter, 2009). In this review, we examine the information that has been revealed by the sequencing of the genomes of *P. ananatis* strains isolated from numerous habitats. Key areas of the lifestyle of this important phytopathogen, including ecological diversification, pathogenicity and biotechnological applications, are discussed. We found that the plasticity of the *P. ananatis* genome allows it to be an adaptable, multi-faceted bacterium that not only survives, but thrives, in numerous ecological niches and lifestyles.

PANTOEA ANANATIS IN THE GENOME SEQUENCING ERA

To date, the genomes of 22 *P. ananatis* strains have been sequenced (Table 1). The main focus of these genome sequencing projects has been on phytopathogenic isolates, including strains from pineapple, rice, *Eucalyptus*, cotton, maize and onion (Adam *et al.*, 2014; Choi *et al.*, 2012; De Maayer *et al.*, 2010; Medrano and Bell, 2015; Weller-Stuart *et al.*, 2014). However, a variety of endophytic isolates (Midha *et al.*, 2016; Sheibani-Tezerji *et al.*, 2015), plant growth-promoting strains, isolates with potential biotechnological and biological control applications (Gasser *et al.*, 2012; Gkorezis *et al.*, 2016; Hara *et al.*, 2012; Kim *et al.*, 2012; Megías *et al.*, 2016; Shi *et al.*, 2015; Smith *et al.*, 2013; Wu *et al.*, 2016) and a clinical isolate (De Maayer *et al.*, 2012b) have also been sequenced.

The genomes of *P. ananatis* strains are, on average, 4.81 megabases (Mb) in size and range between 4.34 Mb (*P. ananatis* S6) and 5.25 Mb (*P. ananatis* DAR 76143). Between 4026 (*P. ananatis* LMG 20103) and 4698 (*P. ananatis* PA4) proteins are encoded on the genomes. The genome of all strains incorporates a single large chromosome and a universal large plasmid, LPP-1, which ranges in size between 280.8 and 352.8 kilobases (kb) and codes for between 238 and 320 proteins (Choi *et al.*, 2012; De Maayer *et al.*, 2012a; Weller-Stuart *et al.*, 2014). The presence of additional plasmids cannot be excluded (Ismail *et al.*, 2014), particularly in the strains with larger genomes, as the majority of the genomes are draft sequences. The G + C contents of the genomes are relatively similar, with an average G + C content of 53.6%.

ECOLOGICAL DIVERSIFICATION CAN BE LINKED TO THE EXTENSIVE GENOME PLASTICITY OF *P. ANANATIS*

The global distribution of *P. ananatis* strains, the wide range of sources from whence they have been isolated, the different associations with their diverse hosts as pathogens and saprophytes, and their variable metabolic and biological capacities are testament of the extreme versatility of this species. This phenotypic diversification can be linked to the extensive genomic plasticity observed within the species. A pan-genome analysis of eight *P. ananatis* strains has shown that, although there is a large core genome (3876 protein coding sequences) conserved among the eight strains, there is also a sizeable accessory genome (1690 protein coding sequences). The sequencing of an additional strain would add 106 unique protein coding sequences to the open pan-genome of the species (De Maayer *et al.*, 2014). Although the majority of the accessory genome is derived from integrated prophages, a number of the accessory proteins are specific to bacteria that colonize animal, plant or insect hosts and include proteins involved in carbohydrate and amino acid metabolism, adherence to host tissues, protection against plant and animal defence systems and putative pathogenicity determinants (De Maayer *et al.*, 2014). The presence of these accessory proteins hints towards the specialization of particular strains to their different ecological niches, hosts and, potentially, lifestyles.

The role of accessory proteins in determining the lifestyle of a bacterium was demonstrated in a study comparing the genomes of three *P. ananatis* strains isolated from maize seeds. These strains showed 85%–87% similarity in their core genomes. The strains selected were pathogenic, commensal and beneficial to the host, respectively (Sheibani-Tezerji *et al.*, 2015). These phenotypic differences were attributed to the integration of mobile genetic elements, such as phages and transposases, as well as differences in the type VI secretion systems (T6SSs) and type IV pili (Sheibani-Tezerji *et al.*, 2015). Eukaryotic-like protein domains were identified in these strains and included enzymes that increased mutation frequency, allowing bacteria to adapt to changing environmental conditions. Other eukaryotic-like protein domains included proteins that play a role in adhesion and virulence (Sheibani-Tezerji *et al.*, 2015).

A major contributing factor in the adaptability of *P. ananatis* strains may be the presence of the universal plasmid (LPP-1) which is derived from a plasmid that is ancestral to the genus *Pantoea* (De Maayer *et al.*, 2012a). Within both the genus and species, LPP-1 has undergone extensive genetic diversification with the insertion of several phage and mobile genetic elements (De Maayer *et al.*, 2012a). Many of the genes encoded on LPP-1 play a role in determining the phenotype of this bacterium. These various phenotypes include metabolic diversity, iron and nitrogen assimilation, resistance to selected antibiotics and heavy metals, and host–microbe interactions (De Maayer *et al.*, 2012a).

Another key factor in the diversification of *P. ananatis* is the presence of an Integrative and Conjugative Element (ICE*Pan*), an integrating and excising mobile genetic element, which was observed in a subset of strains [five of eight genome sequenced strains and 24 of 46 strains as determined by polymerase chain

Table 1 Currently sequenced *Pantoea ananatis* genomes.

Strain	Assembly	Genome size (Mb)	G + C (%)	Status	No. CDSs	Interest	Source	Reference
P. ananatis AJ13355	GCA_000270125.2	4.88	53.7	Complete	4223	Biotechnological	Soil	Hara *et al.* (2012)
P. ananatis AMG521	GCA_001465955.1	4.88	53.1	Draft	4315	Plant growth promoter	Rice paddy	Megías *et al.* (2016)
P. ananatis B1-9	GCA_000285975.1	5.12	53.5	Draft	4566	Plant growth promoter	Rhizosphere of onion root	Kim *et al.* (2012)
P. ananatis BD442	GCA_000709995.1	4.8	53.6	Draft	4330	Plant pathogen	Onion seed	Weller-Stuart *et al.* (2014)
P. ananatis BRT175	GCA_000475035.1	4.85	53.7	Draft	4336	Antibiosis	Strawberry	Smith *et al.* (2013)
P. ananatis CFH 7-1	GCA_001187705.1	4.6	53.1	Draft	4094	Plant pathogen	Cotton boll	Medrano and Bell (2015)
P. ananatis DAR 76143	GCA_000467085.1	5.25	53.4	Draft	*	Plant pathogen	Rice	*
P. ananatis LMG 20103	GCA_000025405.2	4.7	53.7	Complete	4076	Plant pathogen	*Eucalyptus*	De Maayer *et al.* (2010)
P. ananatis LMG 2665^{T}	GCA_000661975.1	4.94	53.4	Draft	4403	Plant pathogen	Pineapple fruitlet	Adam *et al.* (2014)
P. ananatis LMG 5342	GCA_000283875.1	4.91	53.3	Complete	4345	Clinical isolate	Human wound	De Maayer *et al.* (2012a)
P. ananatis NS296	GCA_001475715.1	4.73	53.5	Draft	4272	Endophyte	Rice seed	Midha *et al.* (2016)
P. ananatis NS303	GCA_001476115.1	4.73	53.5	Draft	4266	Endophyte	Rice seed	Midha *et al.* (2016)
P. ananatis NS311	GCA_001475725.1	4.72	53.5	Draft	4227	Endophyte	Rice seed	Midha *et al.* (2016)
P. ananatis PA13	GCA_000233595.1	4.87	53.6	Complete	4403	Plant pathogen	Rice grain	Choi *et al.* (2012)
P. ananatis PA4	GCA_000710015.1	5.16	53.6	Draft	4698	Plant pathogen	Maize	Weller-Stuart *et al.* (2014)
P. ananatis PaMB1	GCA_000766045.1	4.76	53.8	Draft	4223	Plant pathogen	*	*
P. ananatis R100	GCA_001543055.1	4.86	53.6	Complete	4289	Antibiosis	Rice seed	Wu et al. (2016)
P. ananatis RSA47	GCA_001475885.1	4.74	53.5	Draft	4268	Endophyte	Rice seed	Midha *et al.* (2016)
P. ananatis S6	GCA_001369355.1	4.34	54.1	Draft	4375	Endophyte	Maize seed	Sheibani-Tezerji *et al.* (2015)
P. ananatis S7	GCA_001369375.1	4.49	54.0	Draft	4516	Endophyte	Maize seed	Sheibani-Tezerji *et al.* (2015)
P. ananatis S8	GCA_001369395.1	4.48	54.1	Draft	4528	Endophyte	Maize seed	Sheibani-Tezerji *et al.* (2015)
P. ananatis Sd-1	GCA_000582575.1	4.93	53.3	Draft	4332	Biotechnological	Rice seed	Ma *et al.* (2016)

The strain, isolation source and reason for sequencing are indicated. The sizes of the genomes, average G + C content (%), number of proteins (CDSs) encoded on the genome and sequencing status are shown, as per the National Center for Biotechnology Information Genome Assembly and Annotation report (www.ncbi.nlm.nih.gov/genome/genomes/2606).

*Data unavailable.

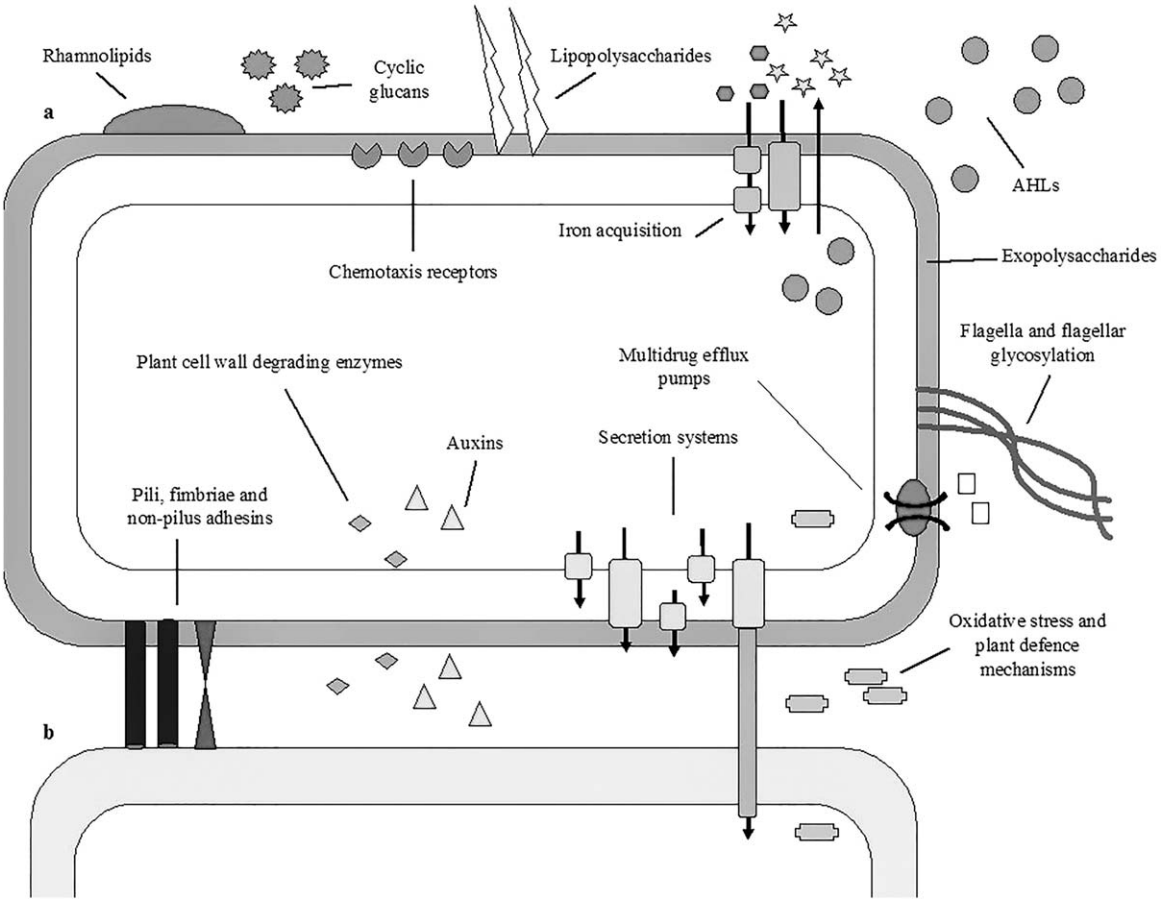

Fig. 1 Putative plant-pathogenicity factors of *Pantoea ananatis*. The pathogenicity determinants of *P. ananatis* (a) when infecting a host plant cell (b). The secretion systems include Tat and Sec secretion systems, as well as the type I secretion system (T1SS), T5SS and T6SS. AHLs, acyl-homoserine lactones.

reaction (PCR) amplification of conserved ICE*Pan* genes] isolated from a wide variety of hosts and geographical origins (De Maayer *et al.*, 2015). *In silico* analyses showed that ICE*Pan* encodes various proteins that may play a role in antibiosis and the stress response, which probably enables *P. ananatis* to occupy diverse environmental niches (De Maayer *et al.*, 2015). For example, orthologues of alternative RNA polymerase σ factors that play a role in overcoming stress factors, such as starvation, heat and cold shock, pH and oxidative stress and DNA damage, are present on ICE*Pan* (De Maayer *et al.*, 2015). A putative novel antibiotic and bacteriocins encoded on ICE*Pan* may also confer a competitive advantage over other organisms occupying the same environmental niche (De Maayer *et al.*, 2015).

NEW INSIGHTS INTO THE PATHOGENICITY OF *P. ANANATIS*

Early genomic evidence revealed that many of the typical pathogenicity determinants found in well-known plant pathogens, such as *Pseudomonas*, *Xanthomonas*, *Ralstonia* and the more closely related enterobacterial phytopathogens *Erwinia amylovora* and *Pectobacterium* spp., such as the type II secretion system, Hrp type III secretion system and phytotoxins, such as coronatine, are absent from the genomes of *P. ananatis* strains (Coutinho and Venter, 2009; De Maayer *et al.*, 2014). However, orthologues of other predicted pathogenicity determinants (Fig. 1), such as flagella and fimbriae biosynthetic proteins, non-fimbrial adhesins, amylovoran/stewartan-like exopolysaccharide and potential cell wall-degrading enzymes (CWDEs), are encoded on the genomes of many *P. ananatis* strains (De Maayer *et al.*, 2014; Ma *et al.*, 2016; Miller *et al.*, 2016). Recent genetic and mutagenic analyses have also contributed to our understanding of the mechanisms underlying *P. ananatis* phytopathogenesis. For example, *P. ananatis* strains encode up to three T6SSs, which may play a role in pathogenesis in both plant and animal hosts (De Maayer *et al.*, 2011; Shyntum *et al.*, 2014). The first and second T6SSs appear to be universal among *P. ananatis* strains and are hypothesized to play a role in antibiosis, fitness and niche adaptation (Shyntum *et al.*, 2014). It is likely that the second T6SS locus, which is incomplete, arose through the duplication of the first locus, whereas the third locus,

which is plasmid borne, was acquired through horizontal gene transfer (De Maayer *et al.*, 2011). In a study conducted by Shyntum *et al.* (2015), it was shown that the first locus is fully functional and plays a role in pathogenicity in plant hosts, specifically onion seedlings, and is also an important factor in intra- and interspecies bacterial competition.

Motility plays a crucial role in the infection process of many well-characterized plant pathogens, such as *Ralstonia solanacearum*, *Pseudomonas syringae* and *Xanthomonas oryzae* pv. *oryzae* (Kang *et al.*, 2002; Meng *et al.*, 2011; Shen and Ronald, 2002), and it has been shown to play a similar role in *P. ananatis* (Weller-Stuart *et al.*, 2016). Research on *P. ananatis*–onion seedling interactions demonstrated the need for functional flagella in initial attachment and pathogenicity. Both the structure and function of the flagella were disrupted in separate, site-specific mutations, as the actual flagellar filament may play a role in adhesion, whereas swimming motility allows the bacterial cell to overcome the natural repulsive forces that exist between itself and a surface, and also allows the cell to respond to chemotactic signals in the environment (O'Toole and Kolter, 1998; Ramos *et al.*, 2004). The flagellar filament has also been shown to be subject to flagellar glycosylation, which may play a role in the avoidance of host recognition during infection, host specificity, attachment and virulence (De Maayer and Cowan, 2016; Logan, 2006). Flagellar glycosylation occurs when N- and O-linked carbohydrates are added to flagellin, the repeating major subunit of the filament, to change both its antigenic properties and function (Takeuchi *et al.*, 2003). Twitching motility also plays a pivotal role in allowing *P. ananatis* to spread and colonize the surface of the leaf once attachment has occurred (Weller-Stuart *et al.*, 2016). Deletion mutations in the type IV pilin major subunit, as well as the ATPase responsible for retracting type IV pili during twitching motility, demonstrated that, although the role of type IV pili in attachment may be complemented by other pili, such as type I and type III pili, twitching motility is instrumental in the spread of *P. ananatis* across the surface of a leaf (Weller-Stuart *et al.*, 2016). Motility is thus crucial to the infection process in *P. ananatis*.

Plant CWDEs break down one of the primary defences of the plant cell, namely the cell wall. In order to cause disease, bacteria commonly need to breach this barrier and gain entry into the plant cell (Esquerre-Tugaye *et al.*, 2000). All analysed *P. ananatis* strains have several CWDEs, including a putative xylanase, pectin acetylesterase, cellulase and two polygalacturonases (De Maayer *et al.*, 2014). The lignocellulose-degrading strain *P. ananatis* Sd-1 has an unusually high number of carbohydrate-active enzymes among members of the species, including enzymes required for the degradation of cellulose and hemicellulose (Ma *et al.*, 2016). Included in its arsenal of CWDEs are 59 glycoside hydrolases, 25 carbohydrate esterases, 10 cellulases and two polysaccharide lyases (Ma *et al.*, 2016). *Pantoea ananatis* is thus well equipped to degrade the integrity of the plant cell wall and cause disease in its host.

Little is known about how *P. ananatis* causes disease in animal hosts. In humans, infections by *P. ananatis* usually occur in immunocompromised individuals or neonates, where infections can result in bacteraemia (De Baere *et al.*, 2004; Van Rostenberghe *et al.*, 2006). Genomic factors which have been suggested to play a role in animal colonization and infection include adhesins, the T6SS and type I fimbriae (De Maayer *et al.*, 2014; Shyntum *et al.*, 2014). All analysed *P. ananatis* strains also have *rhlA* and *rhlB* genes which are required for the biosynthesis of a rhamnolipid (Smith *et al.*, 2016). This glycolipid is involved in the production of a biosurfactant that not only enables swarming motility, but is also cytotoxic to the bacteriovorous grazing amoeba *Dictyostelium discoideum*, and may thus enable *P. ananatis* to establish infections in humans (Smith *et al.*, 2016). *Dictyostelium discoideum* is often employed in mammalian pathogenicity trials as many of the *D. discoideum* genes encoded on its genome are homologous to human genes and, as a result, its cellular response to pathogenicity factors is similar to that of mammalian cells (Pan *et al.*, 2011).

Quorum sensing is a highly regulated population density-dependent method of regulation of gene expression within a bacterial cell (Morohoshi *et al.*, 2011). Generally speaking, quorum sensing comprises a LuxI homologue, which is an autoinducer synthase and is responsible for the synthesis of the signalling molecules, namely acyl-homoserine lactones (AHLs), and a LuxR homologue, which is the AHL receptor (von Bodman *et al.*, 2003). *Pantoea ananatis* has two LuxI/R homologues, namely EanI/R and RhlI/R (Sibanda *et al.*, 2016). The specific AHLs that are synthesized by *P. ananatis* are *N*-hexanoyl-HL, *N*-heptanoyl-HL and *N*-octanoyl-HL, with the most abundant of the three being *N*-hexanoyl-HL (Pomini *et al.*, 2006). *N*-Heptanoyl-HL and *N*-octanoyl-HL are uncommon in that they are used both as signalling substances and as antimicrobials against Gram-positive bacteria. This may give *P. ananatis* a competitive advantage in its natural environment (Pomini and Marsaioli, 2008). It has been shown that quorum sensing in *P. ananatis* also plays a role in exopolysaccharide biosynthesis, biofilm formation, pathogenicity, cell aggregation and the biosynthesis of hydrolytic enzymes, such as extracellular alkaline phosphatase (Jatt *et al.*, 2015; Morohoshi *et al.*, 2007, 2011; Sibanda *et al.*, 2016).

PANTOEA ANANATIS IN THE AGE OF BIOTECHNOLOGY

Although much *P. ananatis* research has focused on pathogenicity on various plant hosts, this bacterium also provides us with an array of beneficial characteristics that we have only just begun to investigate. For example, several strains are known to aid the growth of their host plants, such as poplar (Gkorezis *et al.*, 2016), onions (Kim *et al.*, 2012), papaya (Thomas *et al.*, 2007) rice (Megías *et al.*, 2016; Sanchez-Matamoros *et al.*, 2013) and red pepper, and can increase crop yield up to three times (Kim *et al.*,

2012). Several *P. ananatis* strains are capable of phosphate solubilization (Kim *et al.*, 2012; Megías *et al.*, 2016), whereby organic and inorganic forms of phosphorus are solubilized and converted into a bioavailable form for plant root growth, seed formation and major metabolic processes, such as photosynthesis and respiration (Sharma *et al.*, 2013). *Pantoea ananatis* can also promote plant growth through the production of cellulose (Megías *et al.*, 2016) and indole acetic acid (IAA) (Kim *et al.*, 2012; Megías *et al.*, 2016). The production of bacterial cellulose aids in inter-domain attachments and biofilm formation, allowing growth-promoting bacteria to effectively deliver growth-promoting agents to their host plant (Augimeri *et al.*, 2015). IAA is a phytohormone that can have both beneficial and deleterious effects on the host plant (Spaepen *et al.*, 2007). When produced in the correct concentrations, IAA aids the plant in cell division and enlargement, tissue differentiation, root proliferation and responses to light and gravity (Spaepen *et al.*, 2007).

Potential applications of *P. ananatis* in bioremediation and biofuel production have also been suggested. Strains of *P. ananatis* have been isolated from aquatic environments near maize fields that were treated with mesotrione, a recalcitrant herbicide commonly used in Europe, Brazil and the USA (Alferness and Wiebe, 2002; Pileggi *et al.*, 2012). *Pantoea ananatis* strains proved effective in the complete degradation of mesotrione in a relatively short period of time (Pileggi *et al.*, 2012). The secretome of *P. ananatis* Sd-1 was analysed and found to encode 154 putative carbohydrate-active enzymes. These enzymes are predominantly responsible for the degradation of cellulose and hemicellulose in plant cell wall polymers (Ma *et al.*, 2016). The secretome also revealed the presence of ligninolytic and lignocellulolytic enzymes and laccases, which have great potential in the lignocellulosic bioenergy industry for the production of biofuels, as well as the decolorization of synthetic dyes (Ma *et al.*, 2016; Shi *et al.*, 2015).

There is increasing evidence that *P. ananatis* can be applied as an effective biological control agent against a range of bacterial and fungal plant pathogens. The sequenced genomes of *P. ananatis* BRT175 and R100 have shed light on the mechanisms of antagonism (Smith *et al.*, 2013; Wu *et al.*, 2016). *Pantoea ananatis* BRT175 produces PNP-1, which is a compound inhibitory against *E. amylovora* (Walterson *et al.*, 2014) and provides protection against *Xanthomonas axonopodis* pv. *vesicatoria* in pepper (Kang *et al.*, 2007). Both *E. amylovora* and *X. axonopodis* pv. *vesicatoria* are causal agents of destructive diseases that have severe economic implications (Johnson, 2000; Ritchie, 2000). The *P. ananatis* R100 genome encodes oxazolomycin and chalcomycin biosynthetic genes, which are antibiotics capable of inhibiting bacterial growth, such as *Agrobacterium tumefaciens*, *Staphylococcus aureus* and *Streptococcus pyogenes* (Kanzaki *et al.*, 1998; Ward *et al.*, 2004; Wu *et al.*, 2016).

CONCLUSIONS

Pantoea ananatis has been well represented in the genome sequencing era with the genomes of 22 strains sequenced to date. The data that we now have available to us have delineated some of the complexities of this species. The plasticity of its genome enables *P. ananatis* to proliferate in numerous environmental niches and to cause disease in a wide variety of hosts. It can be envisaged that, with the availability of the complete gene sets of many different *P. ananatis* strains isolated from different hosts and with distinct lifestyles, and the application of cutting edge molecular tools, we will gain deeper insights into the pathogenicity determinants employed, host range determinants and biology of this important enterobacterium. Future investigations may be able to shed light on how the host genotype may affect the pathogenicity of *P. ananatis*, and what mechanisms this pathogen uses to avoid recognition and the defence response by the broad range of plant hosts it infects. Questions such as these may be answered by combining the wealth of genomic data available with other state-of-the-art molecular tools, such as transcriptomic and proteomic approaches, which could identify differences in the gene expression and protein complement of both the bacterium and host under various circumstances, or with population genetic studies, where the genetic variation within strains is highlighted. We have only just begun to investigate the biotechnological applications of *P. ananatis*, and this is undoubtedly a field of research that merits further investigation.

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