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Genomics update

Genomics of plant-associated microbes

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Plant-associated microbes and plant–microbe interactions can be largely divided in two types: detrimental (pathogenic) and beneficial (symbiotic) interactions. Neutral interactions also occur; this is the case for microbes that live in the rhizosphere (on roots) or phyllosphere (on leaves) without triggering any apparent plant response. Both pathogenic and symbiotic interactions are of relevance to industry because these may impact plant production in negative and positive ways respectively. Several plant-associated microbes produce cell wall-degrading enzymes which may be of industrial use in fermentation of plant products. Here we give a brief update of the current status of genome sequencing and genomics of microbes associated with plants.

Plant-pathogenic microbes

Most sequenced plant-associated microbes that produce cell wall-degrading enzymes exhibit pathogenic interactions with plants. Clear examples of these are the bacteria that belong to the genera *Clavibacter*, *Xanthomonas* and *Xylella* (Table 1). Apart from cell wall-degrading enzymes, bacteria such as *Xanthomonas campestris* may also produce more complex sugars. One of these is xanthan, the main ingredient of xanthan gum, a polysaccharide used as a food additive that is produced by *X. campestris*. With the availability and analysis of several *Xanthomonas* genomes, the biochemical pathways leading to xanthan have been shown to be based on a process involving fermentation of nucleotide sugars converted from intermediates of the pentose phosphate pathway (Vorhölter *et al*., 2008). The genome sequences of a related *Xanthomonas* species that causes the economically relevant rice blast disease, *X. oryzae*, also show presence of secreted plant cell wall-degrading enzymes (Lee *et al*., 2005). A recently sequenced highly pathogenic isolate belonging to this species displays diverse insertion sequences, genome rearrangements and presence of clustered regularly interspersed short palindromic repeats indicating many bacteriophage infections, presumably correlating with the strain-specific adaptations associated with high pathogenicity (Salzberg *et al*., 2008).

Some plant pathogenic bacteria are relevant to industry and science for multiple reasons. *Agrobacterium tumefaciens* (Rhizobiaceae) infects woody rosaceous plants including *Rosa*, but also stone fruit and nut trees and causes cancerous deformations (crown galls) and growth defects. *Agrobacterium tumefaciens* achieves this by transferring a small part of its bacterial genome to the plant and co-opting the plant to produce factors that the bacterium uses for its own subsistence and propagation. The genome sequence of *A. tumefaciens*, published in 2001 (Goodner *et al*., 2001; Wood *et al*., 2001), resulted in a framework to understand how bacteria may evolve to integrate bacterial DNA into the nuclei of eukaryote hosts (Fig. 1). Interestingly, *A. tumefaciens* is able to transfer its DNA into eukaryote hosts through a type IV secretion system in such a way that the host is not alerted to the activity of the bacteria, nor to the fact that it is essentially becoming transformed (McCullen and Binns, 2006). Expression microarray analysis during infection of plants by *A. tumefaciens* has started to shed light on how the bacteria achieve their manipulation of plant hosts (Ditt *et al*., 2006).

Use of *A. tumefaciens* to transform plants or as a heterologous transient *in planta* expression system is not only widespread in plant sciences but is also used to transform industrially important fungi such as *Aspergillus niger* (that produces complex sugar-degrading enzymes and enzymes involved in diverse fermentation processes) and the commonly sold edible mushroom *Agaricus bisporus* (de Groot *et al*., 1998). *Agrobacterium tumefaciens* is therefore commonly used in biotechnological companies and academic research groups for plant and fungal transformation. Plasmids and an exceptional genome organization and maintenance have enabled *A. tumefaciens* to evolve its sophisticated lifestyle, but the evolutionary prerequisites leading to this have been elusive. This year, genome sequences of the two related species *Agrobacterium radiobacter* and *Agrobacterium*

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Table 1. Selection of sequenced genomes of plant-associated microbes, not including lactic acid bacteria.

Organism	Strain	Class	Impact	Disease	Habitat	ENTREZ Genome Project ID	Date
Acidovorax avenae citrulli	AAC00-1	P	A, PP	Bacterial fruit blotch	Host	15708	2007
Agrobacterium radiobacter	K84	P	A, HP, M, PP	None	Host, root nodule	13402	2009
Agrobacterium tumefaciens	C58-UWash/ C58-Cereon	P, NF	A, PP	Plant tumours	Host, root nodule	282/283	2001
Agrobacterium vitis	S4	P	A, PP	Crown gall	Host, root nodule	13372	2009
Ashbya gossypii	ATCC 10895	P, RP	A, BT, PP			13834	2004
Azoarcus sp.	BH72	NF, NP	BT, A	None	Obligate endophyte, soil, host	13217	2006
Bacillus amyloliquefaciens	FZB42		BT, AnP, sPP, A	None	Rhizosphere-colonizing, Soil	13403	2007
Burkholderia ambifaria	MC40-6	P, NF, PD	HP, M, A, BC, BT	Cepacia syndrome	Host, rhizosphere	17411	2008
Burkholderia cepacia	AMMD	NF, PD	BC, A	None	Host, rhizosphere	13490	2006
Burkholderia cepacia	383 (R18194)	P, NF	M, E, BR, AP, HP, BC, A, BP	Necrotizing pneumonia, chronic infection	Host, rhizosphere	10695	2005
Candidatus Phytoplasma aster yellows	AY-WB	P	A, PP	Aster yellows, Witches' Broom	Host	13478	2006
Candidatus Phytoplasma australiense		P	A, PP	Australian grapevine yellows	Host	29469	2008
Candidatus Phytoplasma mali	AT	P	PP, A	Apple proliferation disease	Host	25335	2008
Candidatus Phytoplasma onion yellows	OY-M	P	PP, A	Onions yellow	Host	9615	2003
Clavibacter michiganensis michiganensis	NCPPB 382	P	A, PP	Ring rot, tuber rot, wilting disease	Host	19643	2007
Clavibacter michiganensis sepedonicus	ATCC 33113	P	A, PP	Ring rot, tuber rot	Host	184	2008
Cupriavidus taiwanensis	LMG19424	NF, S	A	None	Host, root nodule	15733	2008
Enterobacter sp.	638		A	None	Endophyte, host	17461	2007
Frankia sp.	Ccl3	NF, NP	A, BT	None	Plant symbiont, soil	13963	2006
Frankia sp.	Mbj2, EAN1pec	NF, NP	B	None	Plant symbiont, soil	13915	2007
Fusarium graminearum	PH-1	MP, P	A, FGI, PP	Head blight		13839	2007
Gluconobacter oxydans	621H	Ac	BT, VitC	None	Plants, fruits, wine, beer	13325	2005
Leifsonia xyli xyli	CTCB07	P	PP, A	Ratoon stunting	Host	212	2004
Magnaporthe grisea	70-15	P	FGI, PP, A	Rice blast		13840	2005
Methylobacterium populi	BJ001		BT, A	None	Host, endophyte	19559	2008
Pectobacterium atrosepticum	SCRI1043	P	A, PP	Soft rot	Host	350	2004
Phytophthora ramorum	Pr102, UCD Pr4	P	A, PP	Sudden oak death	Undefined	12571	2006
Phytophthora sojae	P6497	P	A, PP	Root rot	Undefined	17989	2006
Pseudomonas aeruginosa	PAO1	HP	M, HP, PP, A	Nosocomial infection	Soil, fresh water, host, wastewater	331	2000
Pseudomonas fluorescens	Pf0-1	NP	E, BR	None	Soil	12	2005
Pseudomonas fluorescens	Pf-5	NP	BR, BT, AnP, E	None	Soil, fresh water	327	2005
Pseudomonas putida	KT2440	NP, Sa	E, BR	None	Soil	267	2002
Pseudomonas putida	W619	NP	A, BR,E	None	Endophyte, host, soil	17053	2008
Pseudomonas stutzeri	A1501	D, NP	E, A, BR	None	Host, rice roots, soil	16817	2007
Pseudomonas syringae phaseolicola	1448A/Race 6	P	A, PP	Plant rot, halo blight	Plants	12416	2005
Pseudomonas syringae syringae	B728a	P	A, PP	Plant rot	Plants	323	2005
Pseudomonas syringae tomato	DC3000	P	A, PP	Plant rot, speck disease	Endophyte, host, soil, fresh water	359	2003
Ralstonia solanacearum	GMI1000	P	A, PP	Plant rot, wilting disease	Soil	13	2002
Rhizobium etli	CFN42	NF	A , BT	None	Host, root nodule	13932	2006
Rhizobium etli	CIAT 652	NF	A, BT	None	Host, root nodule	28021	2008
Rhizobium leguminosarum	3841	NF, NP	BT, A	None	Host, root nodule	344	2006
Rhizobium leguminosarum bv trifolii	WSM2304	NP, NF	A, BT	None	Root nodule, host	20179	2008
Ustilago maydis	521	P	A, FGI, PP	Corn smut		1446	2007
Xanthomonas axonopodis pv. *citri*	XV101, 306	P	A, PP	Citrus canker	Host	297	2002
Xanthomonas campestris campestris	8004	P	A, PP	Black rot, citrus canker	Host	15	2005
Xanthomonas campestris campestris	ATCC 33913/ B100	P	A, PP	Black rot	Host	296/ 29801	2002/ 2008
Xanthomonas campestris vesicatoria	85-10	P	A, PP	Bacterial spot	Host	13649	2005
Xanthomonas oryzae	MAFF 311018	P	A, PP	Leaf blight, rice blight	Host	16297	2006
Xanthomonas oryzae pv. *oryzae*	KACC10331	P	A, PP	Blight disease	Host	12931	2005
Xanthomonas oryzae pv. *oryzae*	PXO99A	P	A, PP	Rice blight	Host	28127	2008
Xylella fastidiosa	M12/ M23	P	A, PP	Citrus variegated chlorosis	Host	17823/ 18457	2008
Xylella fastidiosa CVC	8.1.b clone 9.a.5.c	P	A, PP	Citrus variegated chlorosis, Pierces disease	Host	271	2000
Xylella fastidiosa-grape	Temecula1	P	A, PP	Black rot, citrus canker	Host	285	2003

Adapted from the GOLD Database (http://www.genomesonline.org; March 2009).
A, agricultural; Ac, acidophile; AP, animal pathogen; AnP, antibiotic production; BC, biocontrol; BP, bioremediation of pollutants; BR, bioremediation; BT, biotechnological; D, denitrifying; E, environmental; FGI, Fungal Genome Initiative; FI, food industry; HP, human pathogen; M, medical; MP, mycotoxin producer; NF, nitrogen fixation; NFe, non-fermentative; NP, non-pathogen; P, pathogen; PD, pollutant degrader; PP, plant pathogen; RP, riboflavin producer; S, symbiotic; Sa, saprophyte; sPP, suppression of plant pathogens; vitC, vitamin C production.

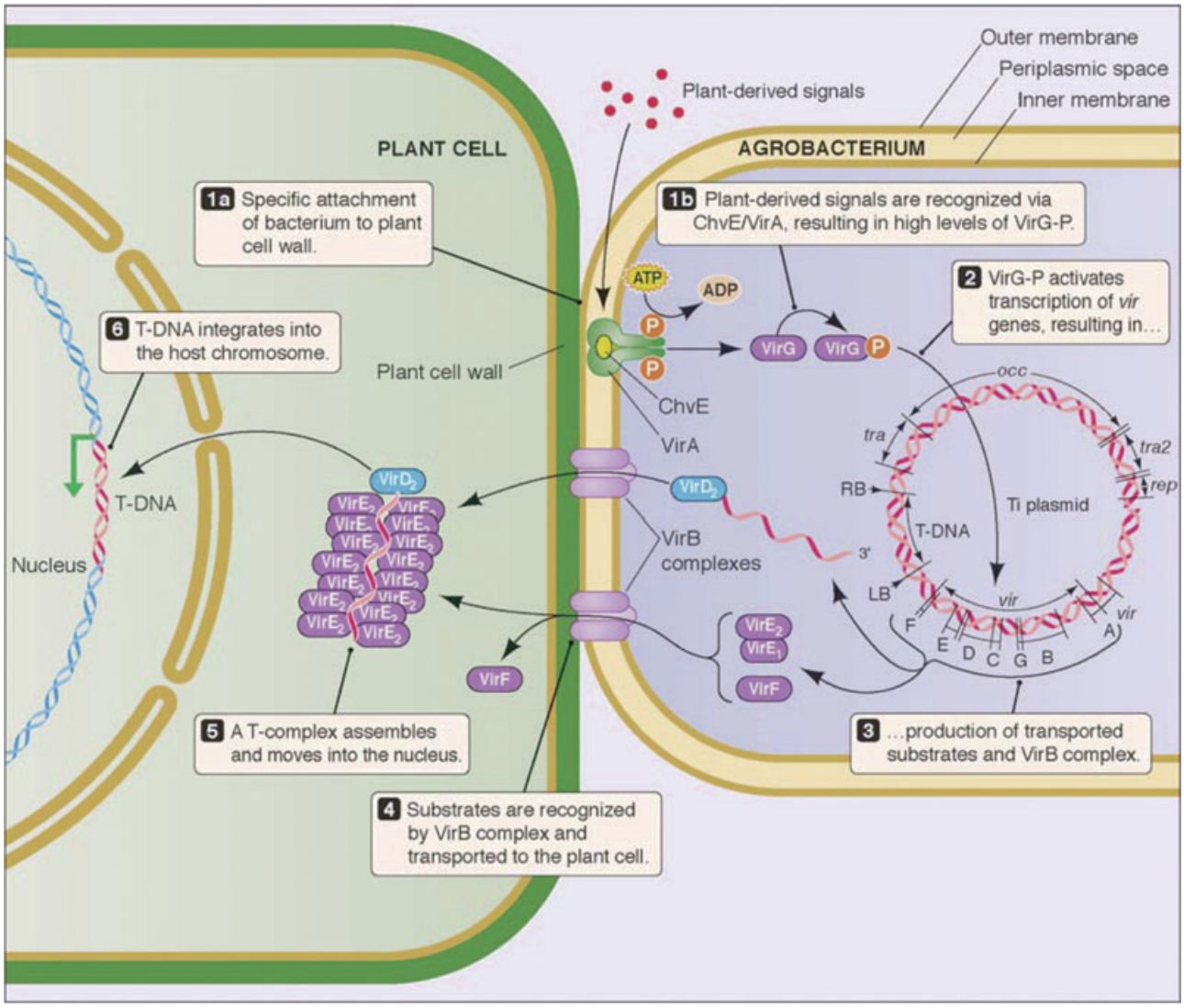

Fig. 1. Schematic example of plant–microbe interactions. *Agrobacterium tumefaciens* responds to plant-derived signals and transfers DNA and proteins into the host plant cell. Reproduced from McCullen and Binns (2006).

vitis, which are also of agricultural and industrial importance, have become available (Slater *et al.*, 2009). *Agrobacterium radiobacter* is commercially being sold as a biological agent for the control of soil-borne plant-pathogenic bacteria, whereas *A. vitis* is an important pathogen of grapes. The published genomes of these two bacteria may help to understand how *A. tumefaciens* may have evolved as a pathogen with complex intragenomic rearrangements and the ability to transfer some of its coding sequences to organisms from other kingdoms of life.

Neutral associations

One group of plant-associated non-pathogenic bacteria belongs to the lactic acid bacteria (LAB; Schroeter and Klaenhammer, 2009). Sequenced genomes of plant-associated LAB include *Lactobacillus plantarum* (Kleerebezem *et al.*, 2003), *Lactococcus lactis* (Siezen *et al.*, 2008), *Pediococcus pentosaceus*, *Leuconostoc mesenteroides* and *Oenococcus oeni* (Makarova *et al.*, 2006). The plant-associated *Lactococcus lactis* strain KF147 was shown to encode numerous enzymes that can degrade complex plant polymers (Siezen *et al.*, 2008). Many LAB are used in starter cultures for fruit and vegetable fermentations (Cogan *et al.*, 2007). A recent study also evaluated the efficacy of LAB isolated from fresh fruits and vegetables as biocontrol agents against the phytopathogenic and spoilage bacteria and fungi *X. campestris*, *Erwinia carotovora*, *Penicillium expansum*, *Monilinia laxa* and *Botrytis cinerea* (Trias *et al.*, 2008).

Microbial growth-promoting symbionts

A different group of bacteria related to *Agrobacterium* within the Rhizobiaceae family are of relevance to industry, not as pathogens but as beneficial symbionts. Bacteria from the genera *Rhizobium* or *Sinorhizobium* contribute to plant production by fixating nitrogen, one of the major elements that are essential for plant growth and agroproduction. It has been suggested several times that it would be very attractive for biotech companies to identify the major genes controlling the trait of nitrogen fixation in selected rhizobia and transfer these to other plant-associated microbes (Zahran, 2001). Since the publication of the first genome of *Rhizobium leguminosarum* (Young *et al*., 2006), 12 more rhizobial genomes are either completed or underway together with four genomes of the closely related *Bradyrhizobium* and two genomes of *Sinorhizobium*. The fact that these symbiotic rhizobia are related to pathogenic *Agrobacterium* sp. makes them ideal objects for comparative expression profiling. Indeed, transcription profiling of soybean nodulation by *Bradyrhizobium japonicum* showed that this bacterium is able to reduce plant defence responses during nodule development (Brechenmacher *et al*., 2008).

Use of the very well-characterized model plant *Arabidopsis* has shown that it is possible to further identify innate defence-associated transcripts that are not directly relating to pathogenic infection. In root colonization experiments with the general plant growth-promoting bacterium *Pseudomonas thivervalensis*, the interactions of roots and bacteria led to an increase of defence-related transcripts in the shoots of plants with colonized roots. Interestingly, plants colonized by *P. thivervalensis* were more resistant to subsequent infections by virulent *Pseudomonas syringae* pv. tomato (Cartieaux *et al*., 2003). Comparison of the genome sequences of pseudomonads, rhizobia and agrobacteria together with host expression profiling will doubtlessly lead to discovery of a wealth of novel bacterial effectors that play roles in symbiotic or neutral plant colonization, pathogenic infection and modulation of host responses. Some of these effectors may also play important roles in infection of humans.

One different class of microbes is the fungi that form symbiotic interactions with trees and shrubs. The basidiomycete *Laccaria bicolor* is an ectomycorrhizal and saprophytic fungus that is commercially used in forest nurseries to promote growth of tree seedlings. Its genome sequence was published recently (Martin *et al*., 2008) and transcriptomes of different tissues and developmental stages have been obtained (NCBI GEO Datasets record GSE9784). Moreover, inoculation studies of scotch pine trees with *Laccaria bicolor* and pathogenic fungi resulted in the identification of genes specifically differentially expressed in the pathogenic, saprotrophic and symbiotic interactions (NCBI GEO Datasets record GSE5410). Such data help to further an understanding of the critical events that are necessary for successful interactions of trees with beneficial symbiotic microbes. A better understanding may contribute to tree management, e.g. by faster screening for optimally symbiotic partners, using biomarkers derived from expression information of both the host and microbe during their interaction. Optimal colonization of tree root systems by *Laccaria* symbionts has beneficial impact on growth and sometimes also protection against stresses including drought-induced salt tolerance and pathogen infection. Interestingly, *Laccaria* encodes enzymes that can hydrolyse sugars and proteins of microbial, decaying organic matter and small arthropod origin, but not of plant cell-wall origin like pathogenic microbes can (Martin and Selosse, 2008).

Plant–microbe interactions relevant to human clinical studies

Plant models can contribute to the study of human health and disease (Jones *et al*., 2008). Plants, like animals, are in possession of an innate immune system that uses pattern recognition receptors in order to detect and eliminate potentially harmful microbes. Some features of the plant and animal innate immune systems show important similarities at the molecular level. Indeed, some pathogens infect plants as well as animals, including humans, by remarkably similar molecular pathways (van Baarlen *et al*., 2007a). These similarities make it possible to use plants as an alternative model host to investigate pathogenicity of human pathogens such as *Staphylococcus aureus*, an important human pathogen of which 30 genomes will soon be available (NCBI Genome Project lists 14 projects as completed, 8 in progress and 8 as draft assembly). *Staphylococcus aureus* genomes are characterized by large between-isolate genetic variation with clear pathological relevance (Melles *et al*., 2004) but the contribution of genetic variation to specific pathological traits are not well understood, partly because testing experimental animals is costly and ethically unfavourable. To accommodate this, *Arabidopsis* plant models can be used to study differential pathogenicity of *S. aureus* isolates (van Baarlen *et al*., 2007b). Upon infection of *Arabidopsis* by *S. aureus* isolates that differ in clinical pathology, the bacteria induce rotting symptoms that differ in severity and morphology (Fig. 2), correlating to a certain extent with disease severity in humans. This forms the basis for experiments where the genetic basis of plant innate resistance against *S. aureus* isolates is investigated and potentially correlated with genomic differences of *S. aureus* isolates. Such a plant model-driven approach may accelerate the identification of microbial drug targets. Functional genomic tools as expression profiling make it

Fig. 2. Two different symptoms (leaf yellowing, upper arrow and wet rot (lower two arrows) induced in *Arabidopsis thaliana* by the human pathogen *Staphylococcus aureus*. Source: B. Thomma and P. van Baarlen, Laboratory of Phytopathology, Wageningen University, the Netherlands.

possible to compare plant and human transcriptomes during infection by microbes such as *S. aureus*. *In silico* tools for such comparative analyses are available for in animal and plant sciences (van Baarlen *et al*., 2008) and the results of such tools can be successfully integrated with other omics and molecular biology tools (van Esse *et al*., 2008).

A similar approach has been used to identify the basis of plant susceptibility to the human pathogen *Pseudomonas aeruginosa*. This bacterium is among the three most often occurring causes of opportunistic infections of human. Because of its clinical importance, a complete genome sequence of highly pathogenic *P. aeruginosa* PAO1 has been available since 2000 (Stover *et al*., 2000). Part of its importance as a pathogen is determined by its resistance to antibiotics. Its relatively large genome sequence of over 6 Mb shows several classes of genes (transcription regulators, protein secretion systems, multi-drug efflux pumps) that are likely to be directly correlating with pathogenicity and antibiotics resistance. Using resistant and susceptible tobacco plants in infection experiments with *P. aeruginosa* PAO1, plant resistance, as in animal hosts, was found to correlate with salicylic acid (the active ingredient of aspirin) accumulation and the availability of micronutrients. Intriguingly, bacteria harvested from the intracellular fluid of plants that were either resistant or susceptible to infection by *P. aeruginosa* showed a differential modulation of bacterial global gene expression (Weir *et al*., 2008). A comparison of genes that were differentially expressed under these two conditions showed that in the resistant plant, especially *P. aeruginosa* genes involved in mobility and attachment, protein secretion and export, secreted factors and small molecule transport were downregulated (Weir *et al*., 2008). These classes of bacterial genes are likely to be involved in resistance against antibiotics and other compounds that are harmful to the bacterial fitness. A similar approach, but now using poplar cuttings in an *in vitro* system, showed that *P. aeruginosa* virulence factors are differentially transcribed in bacteria in presence of the tree host and are necessary for full virulence on poplar (Attila *et al*., 2008). The poplar cuttings responded to bacterial infection by differential transcription of nearly 1800 genes, modulating signal transduction, primary and secondary metabolism and molecular transport. Plant compounds may interfere with pathogenicity, e.g. by inactivating bacterial effectors. Interestingly, similar compounds may also be produced by related bacteria. For instance, at least two completely sequenced strains of the species *P. fluorescens* produce metabolites that suppress rhizosphere plant pathogens (Nelson *et al*., 2002; Paulsen *et al*., 2005). Associative comparisons of expression patterns for other bacteria during antibiosis might yield a better understanding of the function of such bacterial genes that often encode hardly characterized effectors. Furthermore, such genes may turn out to encode essential pathogenicity factors. Several genomes of related pseudomonads have been published in the last 2 years (Table 1). We expect that comparative analyses of the recently published genomes of the plant-pathogenic *P. syringae*, the non-pathogenic but related *Pseudomonas putida* and the non-pathogenic denitrifying *Pseudomonas stutzeri*, together with bacterial expression profiling under relevant *in vivo* (e.g. correlating with pathogenicity) and *in vitro* conditions may contribute to the identification of bacterial factors involved in diverse processes including virulence and pathogenicity, symbiosis, or merely neutral interactions. Some of these factors may turn out to be antibiotics, help cleaning up polluted soils, break down complex contaminating polymers, and may be amenable to large-scale production via genetic engineering.

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