Genomics update

Genomics of plant-associated microbes

Peter van Baarlen1 and Roland J. Siezen2,3,4*
1Host-Microbe Interactomics, Wageningen University, 6709 PG Wageningen, The Netherlands.
2Kluiver Centre for Genomics of Industrial Fermentation, TI Food and Nutrition, 6700AN Wageningen, The Netherlands.
3NIZO Food Research, 6710BA Ede, The Netherlands.
4CMBI, Radboud University Nijmegen, 6500HB Nijmegen, The Netherlands.

Plant-associated microbes and plant–microbe interactions can be largely divided into 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 (Vorhölt 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

*For correspondence. E-mail r.siezen@.cmbi.ru.nl; Tel. (+31) 2436 19559; Fax (+31) 2436 19395.
| Organism                           | Strain                        | Class     | Impact       | Disease                        | Habitat               | ENTREZ Genome Project ID Date |
|-----------------------------------|-------------------------------|-----------|--------------|--------------------------------|-----------------------|-------------------------------|
| Acidovorax avenae citrulli        | AAC001-1                      | P         | A, PP        | Bacterial fruit blot           | Host                  | 15708 2007                    |
| Agrobacterium radiobacter         | K84                           | P         | A, HP, M, PP | None                           | Host, root nodule     | 13334 2009                    |
| Agrobacterium tumefaciens         | CS8-UWash/CS8-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    | None                           | Host                  | 13403 2007                    |
| Azarcoasp.                        | BH72                          | NF, NT    | BT, A        | None                           | Obligate endophyte, soil, host | 13217 2006                  |
| Bacillus amyloliquescens          | FZB42                         | BT, AnP, sPP, A | None          | Rhizosphere-colonizing, Soil |                      | 13400 2007                  |
| Burkholderia ambifaria            | MO40-6                        | P, NF, PD | BC, A        | Cepacia syndrome               | Host, rhizosphere     | 17411 2008                    |
| Burkholderia cepacia              | 383 (R18194)                  | P, NF     | M, E, BR, AP, HP, BC, A | Necrotizing pneumonia, chronic infection | Host, rhizosphere     | 10695 2005                    |
| Candidatus Phytoplasma aster      | AY-WB                         | P         | A, PP        | Aster yellows, Witches’        | Host                  | 13478 2006                    |
| Candidatus Phytoplasma australiana|                               |           |              |                                |                       |                               |
| Candidatus Phytoplasma maii       | AT                            |           | P, PP, A     | Apple proliferation disease    | Host                  | 25335 2008                    |
| Candidatus Phytoplasma onion      | OY-M                          |           | P, PP, A     | Onions yellow                   | Host                  | 9615 2003                     |
| Clavibacter michiganensis         | NCPPB 382                     | P         | A, PP        | Ring rot, tuber rot            | Host                  | 19643 2007                    |
| Clavibacter michiganensis         | ATCC 33113                    | P         | A, PP        | Ring rot, tuber rot            | Host                  | 184 2002                      |
| Cupriavidus taiwanensis           | LMG19424                      | NF, S     | A            | None                           | Host, root nodule     | 15733 2008                    |
| Enterobacter sp.                  | 638                           |           | A            | None                           | Endophyte, host       | 17461 2007                    |
| Frankia sp.                       | Cc3                           | NF, NP    | A, BT        | None                           | Plant symbiot, soil   | 13963 2006                    |
| Frankia sp.                       | Mb2, EAN1pC                  | NF, B     | None         | None                           | Plant symbiot, soil   | 13915 2007                    |
| Fusarium graminearum              | PH-1                          | MP, P     | A, FGI, PP   | Head blight                    | Host                  | 13839 2007                    |
| Gluconobacter oxydans             | 621H                          | Ac        | BT, ViC      | None                           | Plants, fruits, wine, beer | 13325 2005                  |
| Leifsonia xylitii                 | CTBC07                        | P         | PP, A        | Ratoon stunting                | Host                  | 212 2004                      |
| Magnaportha grisea                | 70-15                         | FGI, PP, A| None         | Rice blast                     | Host                  | 13840 2005                    |
| Methylobacterium populi           | BJ001                         | BT, A     | None         | Host, endophyte                | Host                  | 19595 2008                    |
| Pseudomonas bacillispora atrosepticum| SCR1043                  | 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             | 17798 2006                    |
| Pseudomonas aeruginosa            | PAO1                          | HP        | M, HP, PP, A | Nosocomial infection           | Soil, fresh water, host, wastewater | 331 2000                      |
| Pseudomonas fluorescens           | P10-1                         | NP        | E, BR        | None                           | Soil                  | 12 2005                       |
| Pseudomonas fluorescens           | PI-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              | 1448A/Race 6                  | P         | A, PP        | Plant rot, halot blight        | Plants                | 12416 2005                    |
| Pseudomonas syringae syringae     | B728a                         | P         | A, PP        | Plant rot                      | Plants                | 323 2005                      |
| Pseudomonas syringae tomatonia    | DC3000                        | P         | A, PP        | Plant rot, speck disease       | Endophyte, host, soil, fresh water | 359 2003                      |
| Raistonia solanacearum            | GM1000                        | P         | A, PP        | Plant rot, wilting disease     | Soil                  | 13 2002                       |
| Rhizobium etli                    | CFN42                         | NF        | A, BT        | None                           | Host, root nodule     | 13936 2006                    |
| Rhizobium etli                    | CUF62                         | NF        | A, BT        | None                           | Host, root nodule     | 28221 2008                    |
| Rhizobium leguminosumus           | 3841                          | NF, NT    | BT, A        | None                           | Host, root nodule     | 344 2006                      |
| Rhizobium leguminosumus bv trifoli| 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             | 8004                          | P         | A, PP        | Black rot, citrus canker       | Host                  | 15 2005                       |
| Xanthomonas campestris             | ATCC 33913/8004              | P         | A, PP        | Black rot                      | Host                  | 296/ 2002/2008               |
| Xanthomonas campestris             | 85-10                         | P         | A, PP        | Bacterial spot                 | Host                  | 29801 2008                    |
| Xanthomonas campestris             | ATCC 33913/               | P         | A, PP        |                                | Host                  | 13649 2005                    |
| Xanthomonas campestris             | 8004                          | P         | A, PP        | Black rot                      | Host                  | 296/ 2002/2008               |
| Xanthomonas campestris             | ATCC 33913/               | P         | A, PP        |                                | Host                  | 13649 2005                    |
| Xanthomonas campestris             | 85-10                         | P         | A, PP        | Bacterial spot                 | Host                  | 29801 2008                    |
| Xanthomonas campestris             | ATCC 33913/               | P         | A, PP        |                                | Host                  | 13649 2005                    |
| Xanthomonas campestris             | 85-10                         | P         | A, PP        | Bacterial spot                 | Host                  | 29801 2008                    |
| Xanthomonas campestris             | ATCC 33913/               | P         | A, PP        |                                | Host                  | 13649 2005                    |
| Xanthomonas campestris             | 85-10                         | P         | A, PP        | Bacterial spot                 | Host                  | 29801 2008                    |

Adapted from the GOLD Database (http://www.genomesonline.org; March 2009).

A, agricultural; Ac, aciddophile; AP, animal pathogen; AnP, antibiotic production; BC, biocontrol; BR, bioremediation of pollutants; BP, 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; vC, vitamin C production.
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).

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).
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 fixing nitrogen, one of the major elements that are essential for plant growth and agro-production. 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 are 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
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.

Acknowledgement

This work was carried out within the research programme of the Kluyver Centre for Genomics of Industrial Fermentation which is part of the Netherlands Genomics Initiative/Netherlands Organization for Scientific Research.

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