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BS20047: *Pseudomonas syringae* pv. *actinidiae* biovars: a literature review

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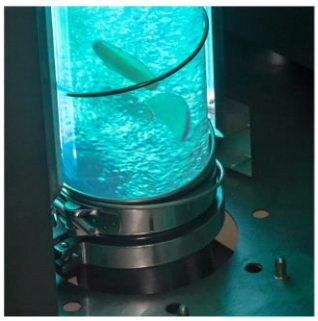


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Contents

Executive summary 1

1 Introduction 2

2 A few definitions of bacterial taxonomy 3

3 Current terminology for Psa 4

4 Evolution of the taxonomy of Psa 7

5 Virulence and biovars 9

6 Acknowledgements 9

7 References 10

Executive summary

BS20047: *Pseudomonas syringae* pv. *actinidiae* biovars: a literature review

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November 2019

Today strains of *Pseudomonas syringae* pv. *actinidiae* (Psa) can be grouped into five biovars. The taxonomy of this pathogen has been evolving rapidly owing to our increased understanding of the phylogenetic relationships between strains. This review first introduces some of the terms used in bacterial taxonomy such as nomenclature, pathovar, biovar, and haplotype. The phylogenetic relationship of the five biovars is then presented, before reviewing the evolution of the Psa taxonomy. The ability of a few strains of different biovars to multiply on or in kiwifruit tissues has been reported but as of today there is no study which demonstrates that strains of some biovars are more virulent than strains of other biovars.

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1 Introduction

Bacterial taxonomy is constantly evolving, because the techniques available to characterise microorganisms are constantly improving and so does our understanding of how organisms relate to each other. In this report, we will be reviewing the nomenclature associated with *Pseudomonas syringae* pv. *actinidiae* (Psa) and the virulence of the different biovars of Psa.

Based on their genomic characteristics strains of *P. syringae* can be grouped in several genomospecies. Because *P. syringae* comprises several genomospecies it is referred to as a complex. Psa belongs to genomospecies 8 of the *P. syringae* complex (Sawada et al. 1999). It has been proposed that strains belonging to this genomospecies are taken out of the *P. syringae* complex and referred to as *P. avellanae* (Gardan et al. 1999). In this case Psa could become *P. avellanae* pv. *actinidiae*. However, this review focuses on Psa taxonomy and not on that of the *P. syringae* complex.

A number of recent studies have been looking at evolution of Psa biovar 3 in a given country or compared genetic markers between strains of biovar 3 isolated in different countries (McCann et al. 2017; Ho et al. 2019). This review does not look at evolution of Psa or evolution of strains within a biovar of Psa; it focuses on the five biovars of Psa currently defined.

Over the years, strains of Psa has been grouped into biovars and haplotypes; the basis and the history of these groupings will be introduced as well as the phylogenetic relationship of the five current biovars of Psa. The final part of this literature review will be dedicated to the link between biovar and virulence.

2 A few definitions of bacterial taxonomy

Bacterial taxonomy comprises nomenclature, classification and identification. Nomenclature and classification are sometimes mistaken for one another. Nomenclature determines how to name a group of organisms. To ensure that new names follow a logical and standardised progression, rules for nomenclature are set out in the International Code of Nomenclature of Bacteria (ICNB) (Dye et al. 1980). However, those rules apply only to taxonomic ranks at the level of subspecies and above (e.g. species, genus, and family). For lower taxonomic ranks such as pathovar, which is an infraspecific rank widely used for the classification of plant pathogenic bacteria, scientists need to follow the 'International Standards for Naming Pathovars of Plant Pathogenic Bacteria'. Taxonomic ranks below pathovars are usually the result of consensus.

At the taxonomic level below that of species i.e. infraspecific level, bacteria can be grouped in pathovars, biovars or haplotypes. There are no formal links between those taxonomic levels. In some cases several biovars or haplotypes can be found in a pathovar. The official definition of a pathovar is 'a strain or a set of strains with the same or similar characteristics differentiated at infraspecific level from other strains of the same species or subspecies on the basis of distinctive pathogenicity to one or more plant hosts' (Dye et al. 1980). In bacteriology a strain is the bacterial population deriving from the isolation of one bacterium. A strain is therefore the equivalent of an isolate. Using pathovar as a model, the definition of biovar is 'a strain or a set of strains with the same or similar characteristics differentiated at infraspecific level from other strains of the same species or subspecies on the basis of distinctive biological characteristics'. A haplotype is a gene or a group of genes that are inherited together. If the genes differ by their DNA sequence we can establish different haplotypes (e.g. *cts* haplotype A and I in Psa).

Classification is about grouping organisms which are similar and establishing relationships between the different groups of organisms. Organisms are grouped based on their characteristics or traits (morphology, behaviour, etc.), which in plants or animals are usually visible and easily detectable. The complete set of observable characteristics is called the phenotype. Bacteria are also classified based on their phenotype, but bacterial characteristics and traits cannot be detected easily. Bacterial phenotypes cannot be determined without doing some tests; for example, a test for the ability to rot a potato tuber, or the ability to grow above 37ºC or on a medium containing 5% salt. Because phenotypic characteristics are coded by genes there is a tendency to bypass the phenotype and analyse the genotype. This can be done using tools such as polymerase chain reaction (PCR) or DNA sequencing.

3 Current terminology for Psa

Today the most commonly used terminology to describe the different groups of Psa is biovar. There is no rule forcing anybody using that terminology; it is used by consensus for ease of communication between scientists, and between scientists and the general public. The word biovar is sometimes omitted, Psa biovar x becoming Psax. The historical changes in the naming of strains of Psa mostly reflect our greater understanding of the diversity of the pathovar *actinidiae*. This is not an uncommon situation, especially when an organism is being studied extensively, as it has been the case with Psa.

All the strains belonging to a biovar are related phylogenetically and share a number of phenotypic characteristics (Figure 1). Initially, the first three biovars were defined as follows: 'Strains from biovar 1 were initially isolated in Japan and Italy prior to 2008, while the strains from biovar 2 were isolated from Korea. These strains share a similar BOX-PCR pattern but have different *cts* sequences. Biovars 1 and 2 can also be separated by DNA sequence differences in other housekeeping (*acn, pfk,* and *gapA*) and effector (*avrD1 and hrpK1*) genes (Chapman et al. 2012). Furthermore, strains from biovar 1 produce phaseolotoxin but not coronatine, whereas strains of biovar 2 produce coronatine but not phaseolotoxin (Han et al. 2003; Chapman et al. 2012). Biovar 3 corresponds to *cts* haplotype 2; it comprises the strains of *P. syringae* pv. *actinidiae* isolated from Italy (after 2008), France, and New Zealand. This definition is from Vanneste et al. (2013).

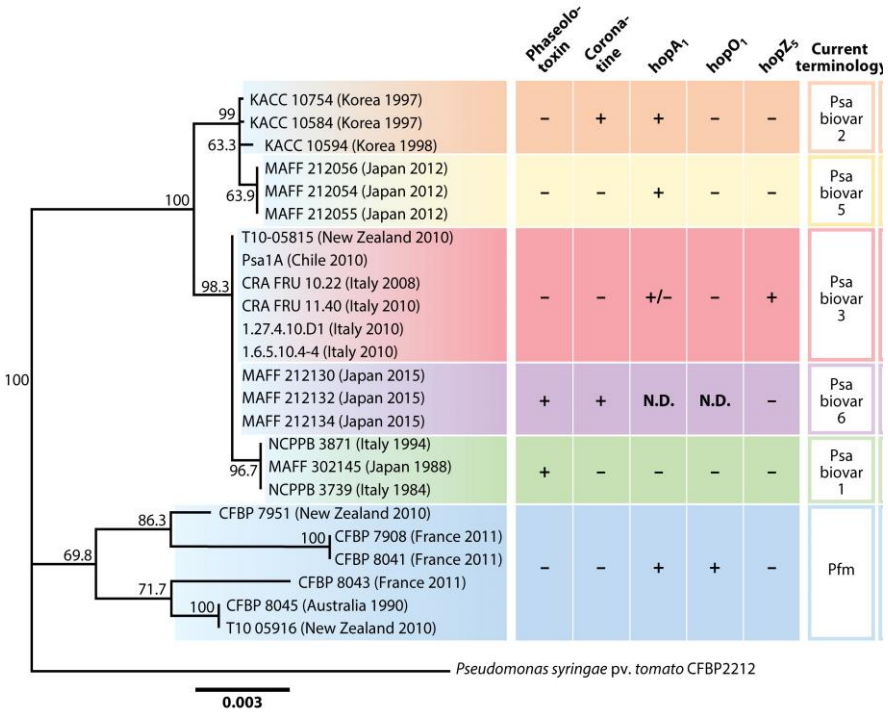

Figure 1. Phylogenetic tree and characteristics of the different biovars of *Pseudomonas syringae* pv. *actinidiae* (Psa). Neighbor-joining tree constructed with the concatenated partial sequences of four housekeeping genes (*gapA, gltA, gyrB*, and *rpoD*). Bootstrap values obtained from 1,000 replicates are indicated at each node. *Pseudomonas syringae* pv. *tomato* was used as an outgroup. The bar represents the number of expected changes per site. Constructing the tree using the concatenated partial sequences of the seven housekeeping genes (*acnB, cts, gapA, gyrB, pfk, pgi*, and *rpoD*) resulted in strains of biovar 6 forming a distinct group separated from strains of biovar 3 (Sawada et al. 2016). The geographic origin and year of isolation are mentioned in parentheses next to each strain name. Abbreviation: N.D., not determined (Reproduced from Vanneste (2017).

In New Zealand in the non-scientific literature (Kiwifruit Vine Health (KVH), industry magazines) Psa-V is used instead of Psa biovar 3. However, there is no publication scientific, legal or otherwise which describes or defines Psa-V or Psa-LV. This terminology was used in New Zealand for the first time soon after 22 February 2011. Before February 2011, the terminology defined in the *New Zealand Plant Protection* paper (*cts* haplotype A and *cts* haplotype I) was being distorted, and became, variously, Italian haplotype and Asian haplotype or Italian strain and Asian or Asian-like strain. At the time Psa-V and Psa-LV was a more appropriate terminology.

The situation for *Pseudomonas syringae* pv. *actinidifoliorum* (Pfm) is different. It has been named following the rules of the 'International Standards for Naming Pathovars of Plant Pathogenic Bacteria'. The name *actinidifoliorum* is a recognised pathovar. Psa biovar 4, Psa4, Psa-LV, PsD and PsHA are obsolete and misleading designations; they should not be used anymore.

Today five biovars of Psa have been described (Table 1). Their geographic distribution is presented in Table 2.

Table 1. Chronology of identification of the different biovars of *Pseudomonas syringae* pv. *actinidiae*.

Biovar	Date of first isolation	Publication date	Reference
1	1984	1989	(Serizawa et al. 1989; Takikawa et al. 1989)
2	1980s	1994	(Koh et al. 1994)
3	2008	2009	(Balestra et al. 2009; Ferrante and Scortichini 2009)
5	2012	2016	(Fujikawa and Sawada 2016)
6	2015	2016	(Sawada et al. 2016)

Biovar 4 identified in 2010 (Everett et al. 2011; Vanneste et al. 2011b) is not mentioned in this Table because strains of this biovar now constitute a new pathovar called *P. syringae* pv. *actinidifoliorum*.

Table 2. Geographic distribution of the different biovars of *Pseudomonas syringae* pv. *actinidiae*.

Country	Biovar	Recorded date of introduction/discovery	Reference
Asia			
Japan	1	1984	(Serizawa et al. 1989; Takikawa et al. 1989)
	3	2014	(Sawada et al. 2015)
	5	2012	(Fujikawa and Sawada 2016)
	6	2015	(Sawada et al. 2016)
Korea	2	1980s	(Koh et al. 1994)
	3	2011	(Koh et al. 2012)
China	3	1983-1984?	(Fang et al. 1990)
Europe			
Italy	1	1992	(Scortichini 1994)
	3	2008	(Balestra et al. 2009; Ferrante and Scortichini 2009)
Turkey	P(3)[a]	2009	(Bastas and Karakaya 2011)
France	3	2010	(Vanneste et al. 2011a)
Portugal	P(3)	2010	(Balestra et al. 2010)
Spain	3	2011	(Abelleira et al. 2011; Abelleira et al. 2014)
Switzerland	P(3)	2011	(EPPO 2011)
Germany	P(3)	2013	(EPPO 2013)
Georgia	P(3)	2013	(Meparishvili et al. 2015)
Slovenia	3	2013	(Dreo et al. 2014)
Greece	3	2014	(Holeva et al. 2015)
Others			
Chile	3	2010	(EPPO. 2011)
New Zealand	3	2010	(Everett et al. 2011; Vanneste et al. 2011b)
Argentina	P(3)	2015	(Balestra et al. 2017)

[a] P(3) probably biovar 3.

4 Evolution of the taxonomy of Psa

In 1989 bacteria that cause bacterial canker of kiwifruit were called *P. syringae* pv. *actinidiae* (Serizawa et al. 1989; Takikawa et al. 1989). This is the first record of this pathovar; the name was suggested following the ICNB rules and was therefore accepted and used by the scientific community.

In 2003 differences between the strains from Japan and those from Korea were observed and recorded (Han et al. 2003). The strains isolated from Korea produced the toxin coronatine while the strains from Japan produced a different toxin: phaseolotoxin. But no name was associated with either group of bacteria.

In 2010, three laboratories came to the conclusion that the strains isolated from Italy after 2008 were different from the strains isolated from Italy before 2008 or the strains isolated from Japan or Korea (Ferrante and Scortichini 2010; Vanneste et al. 2010; Mazzaglia et al. 2011). The three laboratories used different tools to differentiate those strains of Psa. Only in one case was a name given to differentiate those groups (*cts* haplotype A and *cts* haplotype I) (Vanneste et al. 2010).

Analysis of the whole genome sequence data confirmed the previous grouping of the strains isolated until 2012 in four categories (Marcelletti et al. 2011; Mazzaglia et al. 2012; Butler et al. 2013; McCann et al. 2013). The terminology presented in those publications is not being used today, except in some rare cases by the authors of the terminology.

The biovars of Psa were first described in 2013 (Vanneste et al. 2013). The term biovar has been used for grouping of Psa strains to which no other terminology has been attached, e.g. biovar 5 and biovar 6 (Fujikawa and Sawada 2016; Sawada et al. 2016).

Evolution of the taxonomy of Psa is summarised in Table 3.

Table 3. Evolution of the tools and methods used to differentiate the different biovars of *Pseudomonas syringae* pv. *actinidiae* (Psa) in the scientific literature.

Year	Tools and methods for differentiation	Comments	Reference
1989	Physiological and biological characteristics and pathogenicity	First description of the pathovar Psa	(Serizawa et al. 1989; Takikawa et al. 1989)
2003	Biological and molecular tools	First report of genetic diversity in Psa. Strains from Japan produce phaseolotoxin (biovar 1) and those from Korea produce coronatine (biovar 2)	(Han et al. 2003)
2010	rep- PCR (ERIC and BOX); MLST [a] housekeeping genes, PCR for presence of genes coding for toxins and effector proteins	Strains of biovar 3 were shown to be different from those of biovar 1 and 2 but no name was given to any of those groups	(Ferrante and Scortichini 2010)
2010	BOX PCR, cts sequence analysis	Strains isolated from Asia were called *cts* haplotype A (now biovars 1 and 2) and strains isolated from Italy after 2008 were called *cts* haplotype I (now biovar 3)	(Vanneste et al. 2010)
2011	rep-PCR	Strains of biovar 3 were shown to be different from those of biovars 1 and 2 but no name was given to any of those groups	(Mazzaglia et al. 2011)
2011	Whole genome sequence	Differentiation of strains isolated from Japan J-Psa (now biovar 1), strains isolated from Italy before in 1992 I-Psa (now biovar 1), strains isolated from Italy in 2008 I2-Psa (now biovar 3)	(Marcelletti et al. 2011)
2012	MLST analysis of housekeeping genes and effector genes	Psa1 (now biovar 1), Psa2 (now biovar 2), Psa3 (now biovar 3), Psa4 (now *P. syringae* pv. *actinidifoliorum* abbreviated as Pfm)	(Chapman et al. 2012)
2012	Whole genome sequence	Distinguished different groups of Psa equivalent to biovars 1, 2 and 3, and recognised the Chinese origin for biovar3. These groups are called lineages	(Mazzaglia et al. 2012)
2013	Whole genome sequence	Distinguished different variations of biovar 3 based on DNA sequence of ICEs[b]. Also came to the conclusion that strains of Pfm (ex biovar 4) should not be considered as variants of Psa; they were the 'informal names' of PsD and PsHA	(Butler et al. 2013)
2013	Whole genome sequence analysis	Lineages or clades are called Psa J (biovar 1), Psa K (biovar 2), Psa V (biovar 3) Psa LV (biovar 4)	(McCann et al. 2013)
2013	Biochemical and biological characteristics, Molecular characteristics (BOX-PCR) DNA sequencing of housekeeping gene. Pathogenicity assay	First description of Psa biovars 1 to 4	(Vanneste et al. 2013)
2015	Biochemical and biological characteristics, and pathogenicity tests	Biovar 4 renamed *P. syringae* pv. *actinidifoliorum* (Pfm)	(Cunty et al. 2015)
2015	MLST analysis, Biochemical and biological characteristics, and pathogenicity tests	Biovar 4 strains are not Psa, but did not give a name to those bacterial strains	(Ferrante and Scortichini 2015)
2015	Whole genome sequence analysis	Can differentiate strains from China. They are referred to as lineages	(Gallipoli et al. 2015)
2016	Whole genome sequence analysis	Biovar 5 defined. No other name	(Fujikawa and Sawada 2016)
2016	MLST analysis and biochemical characteristics	Biovar 6 defined. No other name	(Sawada et al. 2016)
2017	LAMP[c] assay	Identification of Psa biovars1, 2 and 3	(Ruinelli et al. 2017)

[a] MLST: multi locus sequence typing; [b] ICE: integrative conjugative element; [c] LAMP: Loop-mediated isothermal amplification.

5 Virulence and biovars

Pathogenicity is defined as the ability to cause disease, and virulence as the intensity or the frequency with which a strain will cause disease. The five biovars of Psa characterised today are able to cause the whole range of symptoms attributed to Psa. The assumption that strains of biovar 3 are more virulent than strains of other biovars was the result of observations rather than experimentation. The few experiments which compared the virulence of strains of different biovars did not measure virulence directly but measured the ability and the speed with which strains of different biovars could multiply when inoculated in a kiwifruit plant (McCann et al. 2013; Ferrante et al. 2015).

The virulence of Psa is influenced by the cultivar of kiwifruit (for example, *Actinidia chinensis* var*. chinensis* 'Hort16A' is more susceptible than *A. chinensis* var*. deliciosa* 'Hayward') and by the climatic conditions (relatively cool temperatures and high humidity favour infection and symptom expression). There are no data supporting that differences in symptom expression and virulence of Psa between countries is linked with the biovar of Psa found in those countries. Some of those differences could be due to differences in climatic conditions or in cultivars of kiwifruit being grown. It might be that on some cultivars of kiwifruit some Psa biovars are more virulent than others, but such a differential virulence has not yet been determined. Pathogenicity or virulence cannot be used to determine the biovar of a Psa strain.

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