Phytopathogenic prokaryotes 1962-1992 – an Australasian perspective

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Introduction

Several bacterial plant diseases are most destructive in the lowland humid tropics. Experience of working in Trinidad, West Indies, 37 years ago, and observation at first hand of the destructive potential of Moko disease of banana caused by *Pseudomonas solanacearum* race 2 and of bacterial wilt on a range of vegetable crops, made a lasting impression. *Xanthomonas albilineans*, the cause of leaf scald of sugar cane, which at that time was beginning its movement through the West Indies and the Americas on latently infected planting material (Ogier and Goberdhan 1970), was well characterised and could be grown, albeit slowly and with difficulty, on a suitable isolation medium. However, the minor bacterial pathogens of sugar cane were poorly characterised and their nomenclature was confused and inconsistent. These early contacts with bacterial plant diseases were followed by six years as plant bacteriologist at the Commonwealth Mycological Institute (now IMI) and a return to the sub-tropics at the University of Queensland in 1965.

My purpose is to give an account of the salient developments in phytobacteriology during the past three decades from an Australasian perspective. I have also drawn attention to those bacterial diseases, some well known but others much less well known, which are of great potential importance to Australia and which demand the most rigorous enforcement of exclusion measures.

Phytopathogenic bacteria 1962-1992

Some of the significant developments in phytobacteriology during the past three decades are shown in Table 1. Although different phytobacteriologists would disagree with the importance placed on some entries, there would surely be a consensus on others. The recognition of Mollicutes (Mycoplasma-like organisms) as plant disease agents (Doi *et al.* 1967) was a major development; similarly the biological control of crown gall (New and Kerr 1972), the genetic analysis of pathogenesis and the hypersensitive response, and the discovery of ice nucleation-active bacteria (Maki *et al.* 1974).

In the past three decades there has been considerable growth in understanding of the epiphytic phase of many bacterial plant pathogens. *Erwinia amylovora* and several pathovars of *P. syringae* (Hirano and Upper 1990) and of *X. campestris* possess a prolonged epiphytic phase of significance in disease biology. Much less is known in general about microbial interactions in the phyllosphere, rhizosphere and rhizoplane. Some of the rhizobacteria stimulate growth from seeds or vegetatively propagated planting material and ultimately increase crop yields. Such bacteria are referred to as plant growth promoting rhizobacteria (PGPR), but the effects they produce on plant growth have not been reproducible under all conditions and other rhizobacteria produce a deleterious effect. Much more research will be required to understand the dynamics of microbial interactions in the root zone of plants and their effects on plant growth.

There has been a gradual change from the exclusive use of phenotypic methods in diagnosis of bacterial plant diseases and in the characterisation of phytopathogenic bacteria to a position where phenotypic methods are used in conjunction with DNA-based (genotypic) procedures, or one where total reliance is based on the latter. Molecular methods such as restriction enzyme analysis (Gillings and Fahy 1994) and RFLP analysis (Cook *et al.* 1989) have already made a major impact. Discrimination between strains of a pathogen is potentially far greater with these molecularly-based methods than with phenotypic methods, and there are obvious applications in quarantine and epidemiological investigations However, genotypic methods are often complex, require high capital investment and maintenance costs, and generally require a high level of operator expertise For this reason, phenotypic methods will continue to be widely used in diagnosis, particularly in the developing world

The LOPAT diagnostic scheme developed by Lelliott *et al.* (1966), based on a few well chosen and highly reproducible phenotypic methods which

Table 1 Some milestones in the study of phytopathogenic prokaryotes: 1962-1992[A]

Milestone	Authors
Discovery of hypersensitive reaction	Klement *et al.* (1964)
LOPAT tests for differentiation of fluorescent pseudomonads	Lelliott *et al.* (1966)
Association of mycoplasma-like organisms with yellows-type disease conditions	Doi *et al.* (1967)
Structure of tabtoxin	Stewart (1971)
Biological control of crown gall with *Agrobacterium radiobacter* K84	New and Kerr (1972)
Demonstration of Ti-plasmid in *A. tumefaciens*	Zaenen *et al.* (1974)
Discovery of ice nucleation-active bacteria	Maki *et al.* (1974)
Discovery of aerosol dispersal of potato soft rot bacteria	Graham and Harrison (1975)
Introduction of the pathovar concept in taxonomy of plant pathogenic bacteria	Dye *et al.* (1980)
Determination of virulence genes of *Pseudomonas syringae* pv. *savastanoi* by cloning	Comai and Kosuge (1982)
Demonstration of avirulence genes of *P. syringae* pv. *glycinea*	Staskawicz *et al.* (1984)
Demonstration of hypersensitive reaction and pathogenicity (hrp) genes	Lindgren *et al.* (1986)
Demonstration of RFLP groups in *P. solanacearum*	Cook *et al.* (1989)
Discovery of *harpin*, elicitor of the hypersensitive response in *Erwinia amylovora*	Wei *et al.* (1992)

[A]Based in part on Goto (1992) p. 4.

were simple in application, has been successful in allowing differentiation between the saprophytic fluorescent pseudomonads such as *P. fluorescens* and *P. putida* and the plant pathogens including *P. syringae*, *P. cichorii* and *P. viridiflava*.

Change in nomenclature of phytopathogenic bacteria There have been numerous changes in the nomenclature of phytopathogenic bacteria consequent upon the application of chemotaxonomic and DNA-based methods and these have revealed previously unsuspected heterogeneity in certain genera and new taxonomic affiliations. Differences in cell wall chemistry have been the prime reason for the dispersion of the plant pathogenic coryneform bacteria from the genus *Corynebacterium* into *Clavibacter*, *Arthrobacter, Curtobacterium* and *Rhodococcus* (Table 2). Most recently Zgurskaya *et al.* (1993) have split *Clavibacter* into two with *Rathayibacter* the proposed generic name for the species previously known as *Clavibacter rathayi*, *C. tritici* and *C. iranicus*, and possibly *C. toxicus* associated with ryegrass toxicity in southern Australia. In the case of *Pseudomonas* it is well established that there are five homology groups based upon DNA:rRNA homology (Palleroni *et al.* 1973). Of these, homology group I includes the fluorescent pseudomonads and the type species *P. aeruginosa*. It is to be anticipated that members of the other four homology groups will be transferred to new genera and this process has already begun (Table 3).

With the advent of the Approved List of Bacterial Names (Skerman *et al.* 1980) many former species of *Xanthomonas* and *Pseudomonas* were relegated to the status of pathovars of *X. campestris* and *P. syringae*, respectively, because there were insufficient phenotypic differences by which they could be differentiated independent of their ability to cause disease on specific plant hosts (Dye *et al.* 1980). Subsequent more detailed phenotypic and genotypic investigations have provided evidence that, in some cases, the pathovars of *X. campestris* are distinct and deserving of specific status. *X. campestris* pv. *oryzae*, the cause of bacterial blight of rice, has been elevated to specific status as *X. oryzae*, with two pathovars *oryzae* and *oryzicola*, the latter for the cause of bacterial leaf streak of rice (Swings *et al.* 1990), and similar change in status is expected for other pathovars in the future.

Table 2 Changes in taxonomy and nomenclature of the coryneform bacteria following application of chemotaxonomic methods

Clavibacter Davis *et al.*	e.g. *C. michiganensis* subsp.*michiganensis, C. xyli* subsp. *xyli*
Arthrobacter Conn and Dimmick	e.g. *A. ilicis*
Curtobacterium Yamada and Komagata	e.g. *C. flaccumfaciens* subsp. *flaccumfaciens*
Rhodococcus Zopf	e.g. *R. fascians*
Rathayibacter Zgurskaya *et al.* (1993)	e.g. *R. rathayi*

Table 3 New genera of the pseudomonads based primarily on nucleic acid hybridisation and 16SrRNA sequencing

Previous genus	New genera
Xanthomonas	*Xylophilus* Willems *et al.* (1987) including *X. ampelina*, cause of bacterial canker and necrosis of grape vines
Pseudomonas	*Acidovorax* Willems *et al.* (1990) including *A. avenae*
	Burkholderia Yabuuchi *et al.* (1992) including *B. solanacearum*

Table 4 Fastidious, nutritionally demanding bacterial plant pathogens

Pathogen	Disease(s)	Cultivation on artificial medium
Xylella fastidiosa	Pierce's disease of grapevine, etc.	Wells *et al.* (1987)
Pseudomonas syzygii	Sumatra disease of cloves	Roberts *et al.* (1990)
Clavibacter xyli subsp. *xyli*	Ratoon stunting disease of sugar cane	Davis *et al.* (1980)
Spiroplasma citri	Citrus stubborn	Saglio *et al.* (1973)
Mollicutes (mycoplasma-like organisms)	Numerous hosts: yellows-type disease conditions	Not yet cultured
Prokaryote of uncertain identity	Citrus greening	Uncertain (Da Graça 1991)

Fastidious phytopathogenic bacteria Remarkable progress has been made in the past decade in the cultivation on artificial media of a number of bacterial plant pathogens with complex or specialised nutritional requirements (Table 4). However, the mycoplasma-like organisms, with the exception of *Spiroplasma*, have defied all efforts at cultivation on artificial media.

From the Australasian perspective the development of understanding of the etiology of ratoon stunting disease (RSD) of sugarcane is of most interest (Table 5). This disease causes more losses to sugarcane than any other disease on a worldwide basis. Surveys in Australia have shown that 10-30% of fields may be infected with the disease in some districts and yield losses of up to 40-60% can occur in susceptible cultivars. Annual losses caused by RSD to the Australian sugar industry are conservatively estimated at $10M. For many years the disease was thought to be caused by a virus, until the demonstration by Teakle *et al.* (1973) of the consistent presence of a coryneform bacterium in the vascular tissue of diseased but not healthy sugarcane. The pathogen is very slow growing and requires complex media and was not obtained in culture until 1980 (Davis *et al.* 1980) and later described as *C. xyli* subsp. *xyli* (Davis *et al.* 1984). Many questions of disease biology remain unanswered, which limits the prescription of rationally based control measures. Molecular methods are now to be applied to the study of the pathogen and the disease as part of the research program of the Cooperative Research Centre in Tropical Plant Pathology based in Brisbane.

Since the early 1960s, an apparently infectious disease of cloves (*Syzygium aromaticum*) was observed to be spreading throughout most of Sumatra and West Java, Indonesia, which are the main clove-producing areas of Indonesia. The advent of this major disease problem led in the mid-1970s to the funding of a research program by the Overseas Development Administration, the bilateral aid agency of the British Government. This highly successful collaboration between British and

Table 5 Milestones in the study of ratoon stunting disease of sugarcane

First description in Queensland	Hughes and Steindl (1955)
Association of a coryneform bacterium with disease	Teakle *et al.* (1973);Gillaspie *et al.* (1973)
Bacterium first cultured on artificial medium	Davis *et al.* (1980)
Description of new genus *Clavibacter* and *Clavibacter xyli* subsp. *xyli*	Davis *et al.* (1984)

Table 6 Bacterial plant pathogens which are oligotrophs[A]

Pathogen	Disease	Authors
Rhizobacter daucus	Carrot bacterial gall	Goto and Kuwata (1988)
Rhizomonas suberifaciens	Corky root of lettuce	Van Bruggen *et al.* (1990)

[A]Requiring dilute media: typically peptone has a strongly inhibitory effect.

Indonesian scientists has led to a broadly based understanding of the etiology and epidemiology of the disease. The association of a xylem-limited bacterium with the disease was established and patterns of jump-spread suggested that the disease agent was carried via an airborne pathway, possibly by insect vectors (Bennett *et al.* 1985; Bennnett *et al.* 1987). Discrete outbreaks of this disease have recently been identified at several locations in Sumatra and Java close to natural forest. This suggests that there have been repeated transfers of *P. syzygii* from unknown forest hosts to clove and that cloves should not be planted close to the forest edge (Lomer *et al.* 1992). Although there is both a serological relationship and evidence from DNA hybridisation that the pathogen of Sumatra disease is related to *P. solanacearum*, the two are clearly distinct in phenotypic properties, warranting the creation of the new species *P. syzygii* (Roberts *et al.* 1990). Sumatra disease is transmitted by the tube-building cercopoids, *Hindola fulva* in Sumatra and *Hindola striata* in West Java. *Hindola* spp. (Homoptera: Machaerotidae) are the only insect vectors confirmed so far. Insecticide screening trials against *Hindola* spp have been carried out. Sumatra disease is of interest to Australasian plant pathologists because the host Clove is a member of the same family Myrtaceae as *Eucalyptus*. Nothing is yet known about the possible susceptibility of *Eucalyptus* to this disease.

Oligotrophic phytopathogenic bacteria All phytopathogenic bacteria either require or can at least be cultivated on relatively complex artificial media with the exception of two recently described pathogens *Rhizobacter daucus*, cause of bacterial gall of carrot (Goto and Kuwata 1988) and *Rhizomonas suberifaciens* cause of corky root of lettuce (van Bruggen *et al.* 1990) (Table 6). These bacterial pathogens are oligotrophs by virtue of the fact that they require media that are highly diluted, for example to 10^{-2} or 10^{-3} of normal strength. The oligotrophs are very sensitive to various organic compounds of culture media, but the inhibitory effect of peptone is particularly pronounced. The recognition of oligotrophs as plant pathogens is of great interest. Are there other unrecognised pathogens which require dilute media for cultivation? The usual assumption if plant pathogens cannot be cultivated is that the culture medium requires enrichment with a variety of growth factors present in plant and animal extracts. With oligotrophs, however, the requirement is for dilution rather than enrichment.

The presence of corky root of lettuce in Queensland, Australia, has recently been established (van Bruggen and Jochimsen 1993) and a search in other states is warranted.

Bacterial plant diseases of quarantine importance

Within Australia a few bacterial diseases are of limited distribution and sometimes of quarantine importance between states. For example, bacterial leaf blight of rice caused by *X. oryzae* pv. *oryzae* has been reported in Queensland and the Northern Territory but not in any southern rice-growing area. Bacterial wilt of potato in southern Australia caused by *P. solanacearum* (biovar 2, RFLP group 26, Cook *et al.* 1989) is at present of only sporadic occurrence in certain production areas in Australia. But when the disease does occur there may be devastating losses, serious interference with land usage and quarantine restrictions on the export of seed potatoes from affected areas. Bacterial wilt of

potato has been reported in all states of Australia except Tasmania, with most reports coming from Queensland, New South Wales and Victoria. There appear to be areas in each of these states where the disease is endemic, and other areas where the disease has been introduced on uncertified or one-off certified seed tubers on one or more occasions and subsequently declined. Latently infected seed potatoes continue to serve as the vehicle for introduction into land with no previous history of the disease. For example, during the past three years there has been a series of reports of the disease to the east and south-east of Adelaide, South Australia. Information on the origin of these outbreaks is difficult to obtain. Bacterial wilt of potato was reported in Victoria at Kooweerup and Trafalgar, Gippsland, somewhere around 1911 to 1914 (Harrison 1961), and there have been other reports since. However, the present distribution of the disease is very poorly documented, although well known to at least certain growers. Traffic in seed potatoes is in need of greater regulation to avoid the exceedingly damaging consequences of introducing the disease to new areas.

There are several major bacterial diseases which are not present in Australia and which are of particular importance to Australian agriculture (Table 7). Of these two, citrus canker and Moko disease of banana have been detected on one or more occasions and subsequently eradicated. Moko disease of banana was introduced into Cairns, north Queensland in 1989 on *Heliconia*, an ornamental host. The early detection of the disease in the field and the prompt application of stringent control measures were crucial in eradication of the disease (Hyde *et al.* 1992). Without early access to the RFLP analysis of Cook *et al.* (1989) and restriction enzyme analysis (M. Gillings, BCRI, Rydalmere, unpublished data) precise identification would have been delayed as would have been application of eradication measures *P solanacearum* is a complex species including

Table 7 Some bacterial plant diseases of quarantine importance to Australia

Pathogen	Disease/host	Records in Australia	Present status
Clavibacter michiganensis subsp. *sepedonicus*	Ring rot of potato	None confirmed	–
Xanthomonas campestris pv. *citri*	Citrus canker	Northern Territory (1912)	Eradicated, Broadbent *et al.* (1992)
		Cocos (Keeling) Islands (1981)	Eradicated, Broadbent *et al.* (1992)
		Thursday Island, Torres Strait (1984)	Eradicated, Jones (1991)
		Near Darwin (NT) (1991)	?Eradicated
		Christmas Island, Indian Ocean	Not eradicated, (Shivas 1987)
Pseudomonas solanacearum race 2	Moko disease of banana	Cairns (north Qld) (1989)	Eradicated, (Hyde *et al.* 1992)
Pseudomonas solanacearum biovar 1	Bacterial wilt of *Eucalyptus* spp.	None confirmed (Dianese *et al.* 1990)	–
Erwinia amylovora	Fireblight of apple and pear	None confirmed	–
Erwinia stewartii	Bacterial wilt of maize	None confirmed	–
Xylella fastidiosa	Pierce's disease of grapevine, etc.	None confirmed	–
Xylophilus ampelinus	Bacterial blight of grapevine	None confirmed	–
Prokaryote of uncertain identity	Citrus greening	None confirmed	–

numerous genotypes, several of which are associated with banana but differ greatly in importance as pathogens of banana. This incident is a clear illustration of the superiority of molecular methods, with their much greater power of discrimination between strains, in pathogen identification as compared with phenotypic methods.

Citrus canker has been reported in Australia four times and believed to have been eradicated on each occasion (Jones 1991; Broadbent *et al.* 1992), but a recent outbreak in May 1993 has occurred in the same area of the Northern Territory as that previously affected. There are climatic conditions in certain citrus growing areas of Australia which are highly conducive to the disease and others where conditions would be much less favourable (Broadbent 1992).

Fireblight of apple and pear caused by *E. amylovora* is a major threat to Australian orchardists. Experience of the disease overseas has shown that particular regimes of temperature, humidity and precipitation are associated with disease epidemics. Application of these predictive models to the Australian environment has shown that conditions conducive to the disease occur at least at Orange, New South Wales (Penrose *et al.* 1988).

To the north of Australia there occur diseases of banana about which more needs to be known (Table 8). The disease known locally as **bugtok** or **tapurok** was first reported by Roperos (1965) from the south-west Philippine province of Negros Oriental, where it was found to be widespread in certain cooking bananas. The disease is widespread throughout banana growing regions, in contrast to Moko disease which remains confined to parts of southern Mindanao, mainly in dessert bananas (Rillo 1979).

The symptoms of bugtok are usually confined to the floral raceme, and foliar symptoms are rare or absent. Fruits of affected plants are discoloured red or brown, and this is associated with vascular discoloration which does not usually extend far into the lower part of the fruit stem (Eden-Green 1994).

Blood disease of banana was first reported by Gäumann from the Indonesian island of Sulawesi (then known as the Celebes). The pathogen was described as *"Pseudomonas celebensis"* which is an invalid name because it was not included in the Approved Lists (Skerman *et al.* 1980). The disease was rediscovered in 1987 (Eden-Green and Sastraatmadja 1990) when investigations of a previously unknown disease in West Java were carried out. The symptoms are similar to those of Moko disease, with leaf yellowing, flaccidity and collapse; destruction of fruits, internal vascular discoloration and a reddish-coloured bacterial ooze giving rise to the name blood disease. Unlike Bugtok, infection is systemic and usually spreads throughout the rhizome affecting the young suckers, which may show wilting and act as a source of infection. According to Eden-Green (1994) blood disease is spreading at rates of more than 25 km per year in Java and poses a serious threat to South East Asia unless appropriate quarantine measures are instituted.

Comparative examination of *P. syzygii* and the blood disease bacterium (BDB) with *P. solanacearum* has shown that the former pathogens are

Table 8 Bacterial diseases of banana and clove in South East Asia of quarantine importance to Australia

Disease	Pathogen	Distribution	Relationships
Sumatra disease of cloves (and a few other Myrtaceae)	*Pseudomonas syzygii* Roberts *et al.* (1990) (insect transmitted)	Sumatra and parts of Java (Indonesia)	Shows DNA homology with *P. solanacearum*
Blood disease of banana (similar to Moko disease)	*"Pseudomonas celebensis"*	Java and Sulawesi, Indonesia	Shows DNA homology with *P. solanacearum*
Bugtok or tapurok of cooking bananas	*Pseudomonas* sp. (near to *P. solanacearum*)	Widespread in the Philippines (Zehr and Davide 1969; Eden-Green 1994)	Similar in phenotype to *P. solanacearum* from Moko disease
Moko disease of banana	*P. solanacearum* race 2	Confined to Mindanao, Philippines	–

closely related to *P. solanacearum* but have probably evolved independently. Both show unique phenotypic and genotypic characteristics considered sufficient to warrant the designation of *P. syzygii* and perhaps the redescription of BDB as a new species. The Bugtok pathogen is closely similar in phenotype and genotype to isolates of *P. solanacearum* causing Moko disease, but the evolutionary origin of the Bugtok pathogen is uncertain and the subject of some controversy (Sequeira 1994). Eden-Green (1994) has put forward the hypothesis that Bugtok in smallholder cooking bananas and Moko in dessert banana plantations in the Philippines are in fact two diseases caused by the same organism.

Australia is fortunate in that several of the most important bacterial diseases of plants have not been introduced or become established. The continuation of this favourable situation will require constant vigilance and the strict enforcement of rigorous quarantine measures.

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