

# Henry Tryon—the true discoverer of the potato brown rot pathogen, *Ralstonia solanacearum*

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Published: 19 December 2023

## Cite this:

 Ryley, M. J. (2023)  
*Historical Records of Australian Science*,  
 doi:[10.1071/HR23007](https://doi.org/10.1071/HR23007)

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## ABSTRACT

Within a few years of the establishment of the convict settlement at Sydney Cove, the potato became one of the staple crops of the population due to its relatively high yield and the prior experience of the convicts and free settlers with growing the crop. In 1894, Henry Tryon described a new disease in southern Queensland that caused rapid wilting of plants, a ring of slightly translucent tissue just below the surface of affected tubers, oozing of a thick, white fluid from the ‘eyes’, and ultimately rotting of the tubers. It soon became known as ‘Tryon’s disease’. He found that a microbe (bacterium) was always associated with affected tubers and stems, provided a very brief description of the bacterial cells and named the microbe *Bacillus vascularum solani*. A few years later the American scientist Erwin Frink Smith wrote a paper on a new disease (brown rot) of solanaceous plants including the potato and tomato, in which he called the causal agent *Pseudomonas solanacearum*, now known as *Ralstonia solanacearum*. Smith dismissed Tryon’s prior claim to the discovery of the disease with some of his comments being personal and scathing. Tryon had the last word, however, cloaking his response in restrained and somewhat convoluted tones.

**Keywords:** *Bacillus solanacearum*, bacterial wilt, brown rot, Erwin Frink Smith, Henry Tryon, potato, *Ralstonia solanacearum*, Tryon’s disease.

## Introduction

The potato (*Solanum tuberosum*) was not specifically included in the lists of livestock, provisions, plants and seeds carried on the First Fleet from England or sourced at Rio de Janeiro and the Cape of Good Hope during the voyage to the colony of New South Wales between May 1887 and January 1888. However, it is possible that potato seed and/or tubers were included in the ‘12 baskets of vegetable seed’ carried from England, and perhaps some planting tubers were collected at the ports of call but not catalogued, or officers and others may have privately brought tubers from England.<sup>1</sup>

The potato soon became a vital and ever-increasingly important horticultural crop in Australia. It was grown in all Australian states and generated some of the first interstate trading of agricultural produce. There were no serious disease outbreaks of the crop until towards the end of the nineteenth century, when Henry Tryon, the then assistant curator of the Queensland Museum and later Queensland government entomologist and vegetable pathologist found wilting potato plants and rotting tubers at several sites in south-eastern Queensland.

In this paper I provide a short account of the potato during the early years of Australian colonisation, discuss the details of Tryon’s discovery, and relate his interactions with the American bacteriologist Erwin Frink Smith, who refused to acknowledge Tryon’s claims of prior discovery. I have used mainly on-line resources including books and scientific papers to source relevant material.

<sup>1</sup>Anonymous (2022a).

## The potato in early Australia

Irrespective of the source of planting tubers, the potato was grown by individuals soon after the First Fleet arrived at Sydney Cove in late January 1788. Judge Advocate David Collins (1756–1810) wrote that in the early days of colonisation garden robberies were frequent due to reduced rations, but if the culprit was caught there were serious consequences. In May 1790, a person caught stealing potatoes from the Reverend George Johnson's garden was given 300 lashes and chained to two other miscreants who had robbed the governor's (Arthur Phillip) garden at least seven times in a month.<sup>2</sup>

Severe penalties for stealing potatoes still occurred almost 100 years later. In Victoria, two boys on a hike decided to camp the night at Lilydale and the next morning stole ten potatoes from a nearby field to cook up for breakfast. Unfortunately, the farmer found them around the fire cooking the potatoes then asked a local trooper to pursue the boys for over four miles (~6 km). The two were sentenced to incarceration in Pentridge Prison for a month as well as another month in lieu of a £5 fine (~AUD \$1,094 in 2022)—a hefty sentence considering they did not 'apparently belong to the criminal class'.<sup>3</sup> Justice was not meted out equally, as in 1862 a Mr White of Rylestone was robbed of a load of potatoes by two bushrangers who apparently got away with the crime scot-free.<sup>4</sup>

Potatoes grew well around Sydney and on Norfolk Island. In December 1790, Major Robert Ross (c. 1740–94) wrote that eleven acres (~4.5 ha) of potato had been planted on Norfolk Island and that they were expecting 230–250 bushels of tubers/acre (~20.6–22.4 t/ha) which would reduce a reliance on wheat.<sup>5</sup> By November 1791, there were two acres (~0.8 ha) grown on government farms around Parramatta, and six years later that area had increased to eleven acres (~4.5 ha).<sup>6</sup> In August 1807, 391 acres (~158 ha) had been planted over the previous year around Sydney, and by December 1820 there were estimated to be 550 acres (~223 ha) in the colony.<sup>7</sup> The crop was also being grown successfully in van Diemen's Land (now Tasmania) and the Swan River colony (now Western Australia).

In most years, production exceeded demand. In May 1792, potatoes were being sold at 3d per lb (~0.45 kg) at

markets in Sydney and over a decade later at the equivalent of 2–2.4d per lb.<sup>8</sup> Farmers at Kissing Point on the Parramatta River (in the now Sydney suburb of Putney) seemed to be the major suppliers of vegetable including potatoes to the Sydney market in the early 1800s.

In February 1803, the Secretary of State for War and the Colonies Lord Hobart (1760–1816) wrote to Governor Phillip Gidley King (1758–1808) urging him to encourage settlers to grow more potatoes and yams (*Dioscorea* species), the produce of which could be used to increase the daily rations of store-dependent people.<sup>9</sup> King replied that over the previous two years there had been a significant increase in the growing of potato by the inhabitants,<sup>10</sup> but did not include any data to back up that statement. He also wrote that potatoes, which could be cropped twice in a year, were preferred to yams.<sup>11</sup> His observations are supported by the botanist and collector George Caley (1770–1829) who wrote that during his first visit to the colony (1800) the potatoes were 'very bad and stinking', but of late they 'are much improved'.<sup>12</sup>

In March 1803, Governor King sent a list of non-indigenous (introduced) plants growing in New South Wales to the English botanist and naturalist Sir Joseph Banks (1743–1820), that included the potato varieties Ox Noble, Champion, Small Kidney, and Blue, the first three being in 'general cultivation'.<sup>13</sup> In early Australian newspapers, there are very few articles that provided information on growing potatoes, which suggests that the knowledge of most growers came from their home countries, mostly England and Ireland. A correspondent with the pseudonym of 'A Rustic' did provide some advice especially to 'the lower order of inhabitants' who were 'much dependent on the growth of the potato'.<sup>14</sup>

The potato was a common and staple crop for both the home gardener and the farmer. The *New South Wales Pocket Almanack and Colonial Rememberancer* of 1806 recommended that potatoes should be planted in January in the garden and in the field and would then be ready to harvest in the middle of winter. Planting into dry wheat (*Triticum aestivum*) stubble, where the land was 'light' or in new ground that was covered with a light manure was best. For the farmer, the largest and finest (tubers) were recommended to be used for (animal) feed. In August, potatoes

<sup>2</sup>Collins (1798) chapter 9, paragraph 61.

<sup>3</sup>Anonymous (1858).

<sup>4</sup>Anonymous (1862).

<sup>5</sup>Ross (1892) p. 418.

<sup>6</sup>Hunter (1895) p. 287. Collins (1798) chapter 15, paragraph 14.

<sup>7</sup>Anonymous (1807).

<sup>8</sup>Collins (1798) chapter 27, paragraph 14. Anonymous (1803).

<sup>9</sup>Hobart (1897) p. 42.

<sup>10</sup>King (1897) p. 322.

<sup>11</sup>King (1897) p. 323.

<sup>12</sup>Caley (1897) p. 293.

<sup>13</sup>King (1803).

<sup>14</sup>"A Rustic" (1803).

should be planted ‘for a general summer crop’, and the use of ‘rotten manure’ was to be avoided.<sup>15</sup>

The agriculturalist James Atkinson (1795–1834) remarked that potatoes were a good first crop in upland districts of the colony where maize (*Zea mays*) did not grow well. He recommended planting a row of potato in every fourth row of a wheat crop, but thought that it would never be an important crop because of the high labour involved.<sup>16</sup>

## Production from 1890 onwards

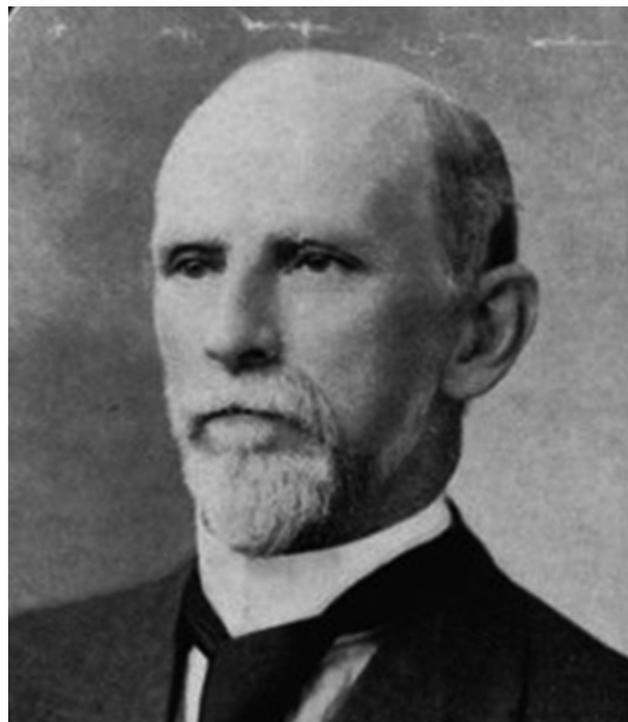
Data on the area and production of potato grown in Australia are sparse prior to 1890, being largely confined to the reports of the early governors of New South Wales. After 1890, data for this section have been sourced mostly from volumes of the *Australian Yearbook*.

Analysis of the ten-yearly data between 1890–1 and 2009–10 for potato reveals that the total area devoted to production in Australia increased modestly compared to other crops such as wheat. In 1890–1, there were 43 200 ha devoted to potato growing in Australia, which is larger than the figure in 2009–10 (36 400 ha), but production increased from approximately 369 kt to >1.27 mt over that period. In 1890–1 the yield was 8.5 t/ha and only increased above 10 t/ha after 1949–50; in 2009–10 that figure was approx. 35 t/ha. Victoria, Tasmania and New South Wales dominated potato production up until the 1970s, but South Australia is now the main producer. Potato is the highest value vegetable in Australia, grossing AUD\$ 717 million in 2016–7.<sup>17</sup>

## The new potato disease

### Henry Tryon’s discovery

Henry Tryon, the first government entomologist (and later vegetable pathologist) in Queensland (Fig. 1) described a disease (commonly called ‘Tryon’s disease’ at the time, at least by Tryon) in April 1894 on potato plants growing at Ravensbourne, near Toowoomba, some suburbs of Brisbane and other parts of south-eastern Queensland.<sup>18</sup> Later in 1897 he told a meeting of farmers at Toowoomba that it had been observed at nearby Ravensbourne as far back as 1891.<sup>19</sup> Tryon believed that the pathogen had been brought



**Fig. 1.** Henry Tryon, ‘former chief Government Entomologist and Vegetable Pathologist, 1929’, John Oxley Library, State Library of Queensland, <https://collections.sliq.qld.gov.au/viewer/IE2859316>.

into Queensland in seed tubers, probably from New South Wales.<sup>20</sup>

The symptoms of the disease were rapid wilting of plants, a ring of slightly translucent tissue just below the tuber surface, and oozing of a thick, white fluid from the eyes. The tissue around these eyes became soft and ‘foecid’, the skin above them gradually collapsed and ultimately the infected tubers became black, soft and foul-smelling (‘offensively odorous’),<sup>21</sup> and finally turned into a ‘seething mass of corruption’.<sup>22</sup> The Queensland plant pathologist John Howard (Jack) Simmonds (1901–1992) wrote that Tryon’s 1894 report was never published in full and that only summaries were provided in *Annual Report of the Queensland Department of Agriculture* and in the overseas journal *Zeitschrift fur Pflanzenkrankheiten*.<sup>23</sup> Tryon’s full report could not be located by the author.

However, lengthy summaries appeared in *Annual Report of the Department of Agriculture for the Year 1893–94* and in an article titled ‘Virulent potato disease’ in the *Brisbane*

<sup>15</sup>Anonymous (1806) p. 13.

<sup>16</sup>Atkinson (1826) p. 38.

<sup>17</sup>Anonymous (2022b).

<sup>18</sup>Tryon (1894a) pp. 2–3.

<sup>19</sup>Tryon (1897).

<sup>20</sup>Tryon (1899) p. 57.

<sup>21</sup>Tryon (1894a) pp. 2–4.

<sup>22</sup>McAlpine (1911) p. 88.

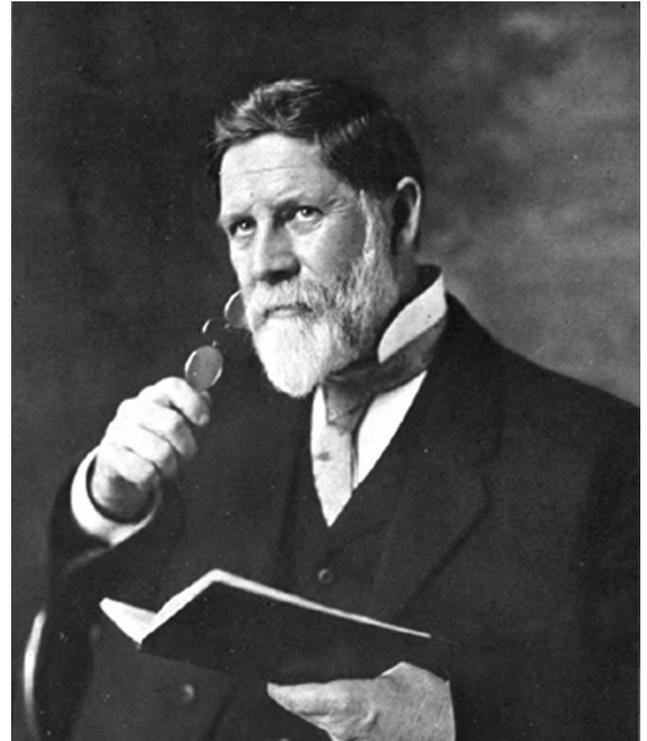
<sup>23</sup>Simmonds (1986) p. 3. Schimper (1895) p. 234.

*Courier* of 5 May 1894, and other newspapers. Tryon described the symptoms as outlined above and wrote that the disease appeared first in individual plants in a crop, and within a few weeks ‘an entire crop can be smitten’. Infected plants never recovered. Five varieties were affected by the disease, and tomato plants (*Solanum lycopersicum*) growing amongst the potatoes also wilted and had discoloured vascular tissue from which a light liquid oozed.<sup>24</sup> Tryon stated that the disease was caused by a bacterium that could live and multiply outside plant tissue including in the soil, and provided advice for control of the disease, including crop hygiene (removal and destruction of infected plants), the use of healthy planting tubers, ‘opening up of the ground’ and liming, ensuring a clean fallow after harvest, not growing potato crops in succession on the same ground and dipping planting tubers in iron sulfate. Those measures were reiterated in his 1899 paper.<sup>25</sup>

Tryon described the bacterium as: ‘A small, living microbe, having an average length of less than one ten-thousandth of an inch (~0.25 µm), resembling in appearance the bacillus of chicken cholera and other organisms’ and they were ‘found clogging up the vessels of stems, roots and stolons, and, in the initial stages of the disease, nowhere else’.<sup>26</sup> He likened it to the pathogen that caused ‘Cobb’s gumming of sugar-cane’, one that Cobb had named *Bacillus vascularum*.<sup>27</sup> Without further description Tryon gave the putative potato brown rot pathogen the name *Bacillus vascularum solani*,<sup>28</sup> and wrote that it was likely that the disease was also present in New South Wales.<sup>29</sup> Only a year later, naturalist Richard Helms (1842–1914) described the symptoms and signs of a disease of unknown cause from the Clarence River region of New South Wales that were the same as those described by Tryon.<sup>30</sup>

### Erwin Frink Smith’s investigation

In 1896, the American plant pathologist Erwin Frink Smith (1854–1927) (Fig. 2) published a bulletin on a bacterial disease of tomato, eggplant and potato.<sup>31</sup> He had initially identified the disease on tomato plants from Mississippi, finding copious quantities of bacterial cells in the vascular stem tissues and successfully inoculating young tomato plants with the bacterium. Later, he inoculated potato plants, the description of the symptoms after inoculation being almost identical to those described by Tryon in



**Fig. 2.** Erwin F. Smith ‘Dean of American plant pathologists’, photographer and date unknown, frontispiece to Whetzel, H. H. (1918) *An Outline of the History of Phytopathology*, W. B. Saunders Co., Philadelphia.

1894. Smith provided a detailed, seven-page description of the morphology and physiology of the causal bacterium, naming it *Bacillus solanacearum*.<sup>32</sup> The reference made to Tryon’s discovery was brief, with Smith stating that from the account of the symptoms he was unable to determine if the ‘Australian disease’ was identical to that in the United States. That comment was mild compared to those that he wrote later.<sup>33</sup>

In 1897, the New South Wales government vegetable pathologist Nathan Cobb (1859–1932) provided a brief description of a potato disease in New South Wales that was characterised by a dark band just below the surface of the tuber; it was probably brown rot. He stated that the microbe always associated with the diseased tubers had been isolated, cultivated and described, but was uncertain whether the microbe in the stems was the same as the

<sup>24</sup>Tryon (1894b).

<sup>25</sup>Tryon (1899) pp. 60–62.

<sup>26</sup>Tryon (1894a) p. 3. Tryon (1899) p. 59.

<sup>27</sup>Cobb (1897) p. 222.

<sup>28</sup>Tryon (1894a, 1897).

<sup>29</sup>Tryon (1894a) p. 2. Tryon (1899) p. 57.

<sup>30</sup>Helms (1895) p. 320.

<sup>31</sup>Smith (1896).

<sup>32</sup>Smith (1896) pp. 10–19. Smith (1914) pp. 193–201.

<sup>33</sup>Smith (1905, 1914).

microbe associated with the dark band in the tubers.<sup>34</sup> There is no doubt that Cobb was referring to Smith's (1896) publication but he was not convinced that Smith's inoculations had proved causality by the bacterium.

### The differences of opinion begin

In early February 1897, Tryon delivered a lecture on the new potato disease at a meeting of the Toowoomba School of Arts. In his lecture, Tryon stated that he was the first person to describe the disease, detect its cause and provide remedies, that Dr Erwan (not Erwin) Smith had resumed the study after learning of the discovery 'at a point where he [Tryon] had left off', and that he had recently received a work that corroborated what he had said. This work is probably Smith (1896). In his lecture Tryon implied that he had made inoculations of potato tubers and tomato plants, but 'whilst all appearance (suggested) that he had succeeded, he would not say as a positive fact that it was so'.<sup>35</sup> Tryon was claiming that he was the first person to describe the symptoms and signs that were associated with the presence of the bacterium, but fell short of proving that it caused the disease. Others were not convinced.

Tryon was fair in his discussion of the subject and particularly about the work on the morphology and physiology of the causal bacterium that Smith and his team had undertaken. He admitted that Smith had gone 'more fully into this aspect' (the morphology and physiology of the causal bacterium) than previously attempted by Tryon. Finally he wrote—the conclusion ... that the American and Australian diseases [of potato were] identical is fully borne out, a verdict that any investigator, endowed with but little less of the spirit of scientific caution exercised by E. M. Smith, might have pronounced even in the meagre light of information, derived from this Queensland source, that partially illuminated the question'.<sup>36</sup>

Smith stated that in the USA the disease occurred on potato, tomato, eggplant (*Solanum melongena*) and tobacco (*Nicotiana tabacum*) and that inoculations on *Solanum nigrum* (black nightshade), *Datura stramonium* (common thornapple) and other plants (all belonging in the family Solanaceae) had been successful.<sup>37</sup> The disease had also been reported from countries in Europe, south-east Asia and perhaps Australia (by Tryon), but he noted that symptoms could be confused with those of blackleg, the causal

agent of that disease being variously named *Bacillus phytophthorus*, *B. atrosepticus* and *B. melanogenum* (all now synonyms of *Pectobacterium atrosepticum*).<sup>38</sup> Smith also provided details on reports of potato and tomato diseases with similar symptoms as far back as 1882 (Italy), including Tryon's report of a disease with symptoms similar to brown rot of potato from Queensland, under the heading 'The Australian Disease'.<sup>39</sup>

He was scathing of Tryon's description and conclusions of the cause of the disease,<sup>40</sup> writing that:

- he (that is Tryon) was an entomologist,
- he never published a (proper) description of the bacterium,
- he never conducted inoculation experiments,
- his initial publication (1895) did not materially help the bacteriologist or pathologist,
- Tryon's name for the bacterium (*Bacillus vascularum solani*) was invalid (a nomen nudum).<sup>41</sup>

Further, he wrote that: 'We shall never know the specific cause of this Australian potato disease is until some *bacteriologist* [Smith's italics] takes hold of the problem'.<sup>42</sup>

### A comparison of the signs and symptoms described by Tryon and Smith

Smith admitted that some of Tryon's descriptions of symptoms were typical of those of brown rot, but others were not, and concluded that Tryon had described a mixed infection or perhaps symptoms of blackleg. However, it is appropriate here to compare the symptoms on potato described by Tryon with those provided in Smith's detailed descriptions and with those of blackleg of potato, caused mainly by *Pectobacterium atrosepticum*. It is apparent that the key symptoms and signs of the potato disease(s) described independently by Tryon and Smith are identical and that neither possess the major feature of blackleg, namely a wet, black lesion that extends up the stem from ground level, causing the stem to rot and collapse.<sup>43</sup>

There are only three symptoms/signs in which Tryon's descriptions differ from those documented by Smith. Firstly, he reported that the foliage of affected plants became chlorotic and died, whereas Tryon did not. This is not a significant issue because it is not a symptom confined solely to

<sup>34</sup>Cobb (1897) p. 222.

<sup>35</sup>Tryon (1897).

<sup>36</sup>Tryon (1899) p. 63.

<sup>37</sup>Smith (1914) p. 174.

<sup>38</sup>Smith (1914) p. 175.

<sup>39</sup>Smith (1914) pp. 207–208.

<sup>40</sup>Smith (1914) p. 208.

<sup>41</sup>Smith (1914) p. 208. A nomen nudum is a taxonomically invalid name because the organism was not adequately and correctly described.

<sup>42</sup>Smith (1914) p. 208.

<sup>43</sup>De Boer and Rubio (2016).

infection of potato plants by the brown rot bacterium. The second difference relates to Tryon's report of a sticky, whitish substance oozing from the eyes of infected tubers, that Smith did not report and rejected as a sign typical of that caused by brown rot. However, the exudation of frothy whitish globules from the eyes and to which soil often adheres is a recognised sign of the disease, which is often called 'sore eyes' or 'jammy eyes'.<sup>44</sup>

The third difference is that Tryon reported a foetid smell emanating from rotten potatoes, whereas Smith did not. However, Smith wrote that once tubers infected with *B. solanacearum* (as called) began to rot, secondary bacteria (and fungi) invaded and exacerbated the rotting, so it is very likely that Tryon was describing the smell emanating from tubers initially infected with *B. solanacearum* but later colonised by secondary bacteria and fungi that caused the foul odour.

In his 1911 book *Handbook of Fungus Diseases of the Potato* the Victorian vegetable pathologist Daniel McAlpine (1849–1932) discussed the potato brown rot and provided some extra information on its symptoms, signs and management. He stated that dark, brown streaks extended down the stems (presumably on the outside of the stem) and passed downwards into the underground branches (stolons).<sup>45</sup> This symptom was not mentioned by either Smith or Tryon, but is recognised as a symptom of infection of potato stems by *R. solanacearum*.<sup>46</sup>

## Erwin Frink Smith—his life and studies on bacteria and brown rot

### Life

So, what type of person was Erwin Frink Smith? He was born on 21 January 1854 to a poor farming family near Fulton, New York, and did not attend high school until he was 22, after the family lost their farm. After graduating, he worked in a prison for a time, read widely and became interested in languages, poetry, the physical sciences and botany, and in 1886 received a BSc from the University of Michigan.<sup>47</sup> In the same year he began work as an assistant in the mycological section of the Division of Botany, United States Department of Agriculture (USDA), investigating the cause, biology and management of the then common disease peach yellows that we now know to be caused by the phytoplasma *Candidatus Phytoplasma pruni*.<sup>48</sup> Three years later he was awarded a

Doctor of Science from the same university for his studies on peach yellows and also became the director of the Laboratory of Plant Pathology, Bureau of Plant Industry, USDA.<sup>49</sup>

### Bacteria studies

In the early 1890s, Smith became interested in the role of bacteria as plant pathogens, a concept refuted by many plant pathologists in Europe and England, particularly the German botanist Alfred Fischer (1858–1913) with whom he had an ongoing debate for several years. After conducting a comprehensive review of the literature on bacterial plant pathogens he found that the methodologies used in previous studies were 'not very exact or very convincing'.<sup>50</sup> His arguments and irrefutable proof of pathogenicity convinced most of the doubters. The three volumes of his *Bacteria in Relation to Plant Diseases* laid the groundwork for the study of the identification, biology and pathogenicity of bacterial plant pathogens.

In a memoir of Smith, I. R. Jones wrote that: 'The personal qualities that endeared Erwin F. Smith to the friends and scientific associates of his mature years were evident from his early youth.' Among these were a 'lovable disposition, passion for study, quick idealism, intense devotion to the task in hand, and unalterable integrity'. Another biographer (C .L. Campbell) wrote that Smith conducted his investigations with 'painstaking exactness'.<sup>51</sup> Perhaps it was these qualities that influenced his opinion on the validity of Tryon's claims.

In Smith's classic 1905 publication on bacterial plant pathogens in which he provides in great detail on the methodologies necessary to undertake studies on the identity, biology and pathogenicity of bacteria isolated from plants he states that 'the brief statement of the nature of the behaviour of the organism on nutrient agar ... with a loose statement of its colour and size no longer constitutes a description that describes'. Also, he wrote that: 'The name will only serve to encumber future synonymy and to recall the incapacity of the author'.<sup>52</sup>

### Later potato brown rot studies

In his 1914 publication, Smith provided a synopsis of all the inoculation experiments using *B. solanacearum* (the name he had bestowed on the organism) that he and his assistants had conducted on plants (mostly potato and tomato) from 27 May 1895 until 24 November 1905.<sup>53</sup> For each experiment the source of the bacterial isolate, the test host, the

<sup>44</sup>McAlpine (1911) p. 88. García and others (2019) p. 8.

<sup>45</sup>McAlpine (1911) p. 89.

<sup>46</sup>García and others (2019) p. 7.

<sup>47</sup>Campbell (1983) pp. 21, 23.

<sup>48</sup>Marcone and others (2014) p. 18.

<sup>49</sup>Anonymous (2023).

<sup>50</sup>Jones (1939) p. 24.

<sup>51</sup>Jones (1939). p. 1. Campbell (1983) p. 24.

<sup>52</sup>Smith (1905) p. 3.

<sup>53</sup>Smith (1896) p. 26, Plate 1. Smith (1914) pp. 182–190.

mode of inoculation and the results were recorded, the methods of inoculation being mostly by pricking stems and leaflets with a needle that had been dipped in a bacterial cell suspension and later by injecting similar suspensions using a hypodermic syringe.

Careful perusal of Smith's results reveal that there were only three experiments, conducted on 15 June 1895, 1 June 1896 and 15 June 1896, that hint at success in inducing tuber rot with an isolate of *B. solanacearum* which had been inoculated in potato stems, and on leaflets and leaf petioles.<sup>54</sup> The results of the 15 June 1895 inoculation state that 'the stem and tubers rotted'<sup>55</sup> while the results of the two June 1896 inoculations are depicted in Smith's (1896) paper in figs 3–7 on plate 1 (Fig. 3). Those figures display tubers, with a brown ring of vascular tissue that had been harvested from plants inoculated in stems.<sup>56</sup> The results of all the other inoculations involving potato were recorded as either a failure or merely wilting of inoculated plants.

Also, he stated that 'needle punctures of leaflets of potato produced the disease as readily as those into stems, the only difference being that the organism had a longer distance to travel and consequently the tubers were not reached and destroyed so early'.<sup>57</sup> However, this general statement is partially supported by the results of only three experiments, as outlined above. Apparently, there were no successful inoculations of potato stems using isolates derived from tubers displaying signs and symptoms of brown rot. Inocula for the three successful inoculations were generated from infected stems of either tomato or eggplant.

In Smith's (1905) publication his four 'rules of proof' of pathogenicity of a plant pathogenic bacterium—basically a re-statement of Koch's postulates—are set out. The last rule was—the discovery, re-isolation and identification of isolates from the inoculated tissue and successful comparison with the original isolate.<sup>58</sup> There is no evidence in his 1896 and 1914 publications that Smith adhered strictly to his own rules of proof, particularly 'Rule no. 4.' In a section of his 1914 volume, Smith wrote that *B. solanacearum* had successfully been re-isolated 'from the interior' of potato stems 15" (~380 mm) and 3' (~914 mm) from the site of inoculations,<sup>59</sup> but there is no evidence that he or his team ever recovered *B. solanacearum* from symptomatic tubers that developed on plants whose stems had been inoculated with the bacterium. Perhaps Nathan Cobb's apparent reluctance to accept that the bacterium in the discoloured vascular tissue of stems also caused brown rot of tubers was a valid assessment of the facts.<sup>60</sup>



**Fig. 3.** External and vascular discolouration of potato tubers (nos. 3–7) from plants inoculated with *Bacillus solanacearum* on 15 June 1896, after Smith (1896), Plate I, <https://archive.org/details/bacterialdisease12smit/page/26/mode/2up?view=theater>.

### An analysis of Smith's rejection of Tryon's prior discovery claim

The next question that can be asked is—was Erwin Smith's dismissal of Tryon's work justified? In summary, there is no doubt that Tryon's 1894 report of the symptoms and signs of brown rot of potato predated that of Smith, who started his investigations in May 1895. In his 1899 paper, Tryon claimed that he had 'repeated some of the experiments that relate to the morphological and physiological characteristics of the bacillus' and shown that it was identical to Smith's '*B. solanacearum*',<sup>61</sup> but he did not provide any data on the results of his 'inoculations'.

In his 1899 publication Tryon also wrote a thinly-veiled criticism of Smith's dismissal of his discovery: 'any investigator, endowed with but a little less of the spirit of scientific caution exercised by E. M. Smith, might have pronounced

<sup>54</sup>Smith (1914) pp. 183–184.

<sup>55</sup>Smith (1914) p. 183.

<sup>56</sup>Smith (1896) p. 26.

<sup>57</sup>Smith (1914) p. 179.

<sup>58</sup>Smith (1905) p. 9.

<sup>59</sup>Smith (1914) p. 179.

<sup>60</sup>Cobb (1897) p. 222.

<sup>61</sup>Tryon (1899) p. 63.

even in the meagre light of the information, derived from this Queensland source, that partially illuminated the question'.<sup>62</sup> Although there is no evidence that Tryon successfully inoculated potato plants with the bacterium that were associated with the symptoms on infected plants in the field, there is little doubt that Tryon had described the potato disease brown rot, despite Smith's skepticism.

There is no evidence that Smith and Tryon ever wrote directly to each other about their disagreement, although Tryon mentioned that he had 'been in communication' with Smith prior to the start of the Smith's investigations.<sup>63</sup> Tryon had the last say in this war of words, but it is unlikely that Smith would have ever read them. In the 1917 *Annual Report of the Entomologist and Vegetable Pathologist* he wrote that Smith had considered that his discovery of the potato disease in Queensland was based on insufficient grounds but that 'this suggestion is one that when the matter of rejecting the claims [of Tryon] due to the original discovery is the consideration is entertainable must be repudiated'.<sup>64</sup> Compared to some of Tryon's criticism of some other fellow scientists that convoluted wording was mild.

## The pathogen in Australia

After several name changes the current name for the potato brown rot bacterium is *Ralstonia solanacearum*.<sup>65</sup> Researchers soon realised that there was considerable pathogenic variation amongst isolates of *R. solanacearum* and instituted a system of race and biovar classification based on host specificity. However, the system proved to be inconsistent and inaccurate, so a classification based on molecular analyses is now used. Currently four phylotypes of *R. solanacearum* have been identified based on sequence variation in the ITS region, and twenty sequevars based on partial endoglucanase gene (*egl*) sequences.<sup>66</sup>

*Ralstonia solanacearum* biovar 2 (as called) is usually a minor disease of potato in Australia but can be serious if plants of highly susceptible varieties experience warm and moist soil conditions during their growth. Management includes the use of certified planting tubers, rotation with non-hosts such as summer cereals, growing varieties with resistance, and minimising machinery movement.<sup>67</sup> These practices, including the last mentioned, are similar to those recommended by McAlpine in 1911.<sup>68</sup> So, on-farm plant biosecurity is not a modern concept.

<sup>62</sup>Tryon (1899) p. 63.

<sup>63</sup>Tryon (1899) p. 63.

<sup>64</sup>Tryon (1917).

<sup>65</sup>García and others (2019). The pathogen also causes a disease known as "bacterial wilt".

<sup>66</sup>García and others (2019) p. 8. A phylotype is a cluster of strains sharing a similar sequence, and a sequevar is a cluster of strains with a highly conserved genetic sequence.

<sup>67</sup>Martin and others (2010).

<sup>68</sup>McAlpine (1911) p. 87.

<sup>69</sup>McAlpine (1911) p. 87. Simmonds (1986) p. 3.

## Conclusions

A fair person might call this difference of opinion a draw. Tryon described the symptoms and signs of brown rot, but Smith proved its pathogenicity (with some reservations) and described the bacterium in detail. Two prominent Australian plant pathologists, Daniel McAlpine and John Howard Simmonds were of no doubt that Tryon had described the potato tuber disease later known as wet rot, brown rot, sore eyes and bacteriosis and had demonstrated that it was caused by a bacterium.<sup>69</sup>

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**Data availability.** Not applicable.

**Conflicts of interest.** The author declares no conflicts of interest.

**Declaration of funding.** No funding was provided by any party for the research and preparation of this paper.

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