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Corrigendum to: The discovery of tomato spotted wilt virus

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The author advises of an error in the published paper.

On the fifth page, the plant *Datura stramonium* was wrongly named as *Datura suaveolens*.

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The discovery of tomato spotted wilt virus

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ABSTRACT

The discovery of tomato spotted wilt virus (TSWV) was an important finding in Australian science, involving a self-educated field naturalist and a small team of plant pathologists who had to work in relative academic isolation and with inadequate glasshouse facilities. After its discovery in Melbourne in 1915, TSWV rapidly spread throughout Australia and by 1929, it posed an existential threat to the tomato industry. To address this problem, a joint project between the Waite Agricultural Research Institute and the Council for Scientific and Industrial Research was initiated in 1926. This collaboration, led by University of Adelaide plant pathologist Geoffrey Samuel, was initially turbulent but ultimately highly productive. Within an eight-year period, significant advances were made in understanding the aetiology of the disease, particularly by establishing that it was caused by a thrips-transmitted virus. Aspects of the epidemiology and control of the virus were also elucidated such as investigating alternative hosts of the virus. This research was made possible through substantial improvements in mechanical inoculation techniques.

Keywords: agriculture, alternative hosts, Charles Brittlebank, circulative transmission, CSIR, epidemiology, Geoffrey Samuel, history, plants, review, thrips, tospovirus, vector.

Tomato spotted wilt virus (genus *Orthotospovirus*) is rated the second most important plant virus in the world, reflecting the fact that it has an exceptionally large host range, and it is also cosmopolitan in distribution, occurring throughout temperate, tropical and subtropical climate zones of the world.[1] Tomato spotted wilt disease (Fig. 1) was first noticed in Melbourne, Victoria, in the 1915–6 growing season.[2] This disease remained peculiar to Australia until 1929, when winter cherry (*Solanum pseudocapsicum*) plants raised in a commercial glasshouse in Cardiff, Wales, succumbed to a novel ringspot disease,[3] which was later recognised to be caused by the same pathogenic agent as spotted wilt.[4] Even though tomato spotted wilt virus (TSWV) was discovered in Australia, it is not considered indigenous to this country as it is vectored by non-native thrips species, and it is mainly a pathogen of non-native plant species.[5] Furthermore, phylogeographic analyses suggest that this virus originated in the New World.[6] TSWV was most likely introduced to Australia in importations of living plants, which may have been infested with thrips, as the virus is not seed-borne.[6]

This article reviews pioneering research done on TSWV in Australia during the first half of the twentieth century, and provides insights into the personalities and interactions between those involved. TSWV research began in Melbourne but then continued in Adelaide and involved an initially turbulent but ultimately highly productive collaboration between staff at the Waite Agricultural Research Institute and the Council for Scientific and Industrial Research (CSIR).

[1] Janssen (2022). Pappu and others (2021). Scholthof and others (2011).
[2] Brittlebank (1919).
[3] Smith (1931*a*).
[4] Smith (1932).
[5] Mound (2002).
[6] Resende and Pappu (2021).

Fig. 1. Tomato spotted wilt disease: panel (*a*), close up of infected leaf, showing necrotic ring patterns (marked with red arrow); panel (*b*), yellow, wilting tomato plant (marked with yellow arrow) among a row of healthy tomato plants. Photographs courtesy of the Queensland Department of Agriculture and Fisheries.

The first description of tomato spotted wilt disease is credited to Derbyshire-born Charles Clifton Brittlebank (1863–1945). Brittlebank arrived in Australia as a twelve-year-old child, and briefly lived in Queensland then Tasmania before settling in Victoria with his widowed mother, Ellen, and younger sibling Thomas.[7] In 1885, the Brittlebank family established a dairy farm at Myrniong near Bacchus Marsh and this period on the land stimulated the brothers' interests in natural history. Early subjects of study by the elder of the two siblings included the investigation of evidence of Pleistocene glaciation in nearby Werribee Gorge and compilation of a bird list for Myrniong.[8] Brittlebank was an excellent scientific illustrator and through his involvement with the Victorian Field Naturalists' Club, he met Charles French (1853–1929), senior government entomologist in Victoria, who invited him to illustrate the five volumes of *A Handbook of the Destructive Insects of Victoria*.[9] He was also an egg collector, and was best known by bird-watchers for his detailed and exquisite watercolours of eggs in Archibald Campbell's *Nests and Eggs of Australian Birds*.[10]

Brittlebank did not have a formal scientific training but his life experience as a farmer and an amateur field naturalist was recognised by many (Fig. 2). He became assistant plant pathologist for Victoria under Daniel McAlpine (1849–1932) in 1908, replacing him as government plant pathologist when he retired in 1913.[11] Technically over-age to hold this position, he obtained permanency in the post by challenging the Public Service Commissioner to a boxing match.[12] One of his early duties was to respond to an outbreak of a new disease in tomato that was first observed in Melbourne during the 1915–6 growing season but peaked in severity in 1918–9, when 50% of suburban gardens were destroyed and the disease spread to nearly all parts of Victoria.[13] A causal agent (bacterium or fungus) could not

[7]Much information about Brittlebank has been sourced from Hewish (2006).
[8]Brittlebank (1899). Brittlebank and others (1898).
[9]French (1891–1911). Anonymous (1945).
[10]Campbell (1900).
[11]Anonymous (1945). White (1981).
[12]The boxing anecdote is given in footnote 120 (p. 94) of White (1981). Credibility to this anecdote is provided by Hewish (2006), who lists one of Brittlebank's hobbies in his youth as amateur boxing. The Public Service Commissioner was wise to back down!
[13]Brittlebank (1919).

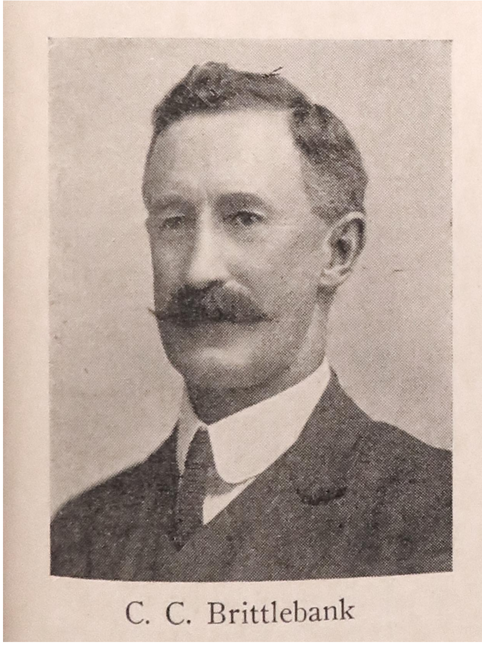

Fig. 2. Portrait of Charles Clifton Brittlebank, from the *Victorian Naturalist*, volume 62, February 1946. Photographer unknown.

be isolated and transmission experiments, including by mechanical inoculation, were unsuccessful. Brittlebank concluded that the disease was most likely physiological in nature, perhaps due to some 'chemical or physical deficiency' of the soil. He must have been a stoic person, as he undertook these investigations while mourning the loss of his only child, Cyril Clifton, who succumbed to influenza in May 1918 while serving in the Australian army on the Western Front in France.[14] Brittlebank retired in 1928 as Biologist in Charge of the Science Branch of the Victorian Department of Agriculture.

During the 1920s, tomato spotted wilt disease rose in prominence to become 'by far the most important disease of this crop in Australia'.[15] There was rapid spread of the pathogen, with the disease reported in South Australia in 1919, in New South Wales in 1920, in Western Australia in 1923, in Queensland in 1926 and finally in Tasmania in 1929.[16] Yield losses were so severe that field cultivation of tomatoes on the Adelaide Plains had to be abandoned in favour of glasshouse crops, and early season crops in the Perth environs were also unsuccessful.[17]

Tomato spotted wilt disease was one of the foundation research priorities of the Division of Economic Botany (the predecessor of the Division of Plant Industries) within the CSIR. The CSIR was created in 1926 by Prime Minister Stanley Bruce's government to enhance federal and state cooperation and to reinvigorate fundamental scientific research by allowing people to work full time on research projects without the distractions of providing routine diagnostic and extension services.[18] Under a cooperative agreement, CSIR paid £1541 for the erection of an insect-proof glasshouse at the Waite Agricultural Research Institute, and £1000 per annum for the salaries and operating expenses of an assistant plant pathologist and technical assistant to work onsite with the university plant pathologist, Geoffrey Graham Samuel (1898–1985).[18] The glasshouse successfully excluded insects, but it was neither heated in winter nor cooled in summer, with ambient temperatures sometimes soaring to 49°C.[19]

Samuel was a graduate of the University of Adelaide, initially enrolling in chemistry and acting as a cadet in the laboratory of Professor Edward Rennie.[20] His time at university was interrupted by service in the 9th Light Horse Regiment (3rd Light Horse Brigade) in Egypt during the closing stages of the Great War (30 April 1918 to 15 February 2019), but he saw little frontline action due to debilitating bouts of bacterial dysentery and malaria that waylaid him in hospital.[21] Upon his return to Australia, he recommenced at university but transferred to botany.[22] His academic talents were recognised by Professor Theodore Osborn, who in December 1922 appointed him as assistant lecturer and demonstrator in the department of botany, using funds from a bequest by the pastoralist and businessman, Peter Waite.[23] For the next two years, he studied diseases of horticultural crops such as brown rot of citrus fruit and pear tree canker, as well as assisting with general diagnostic and taxonomic research.[24] In 1924, Samuel transferred to the Urrbrae Agricultural Research Station, soon to be renamed the Waite Agricultural Research Institute, to become the first full time plant pathologist in South Australia. The CSIR officer appointed to work with Samuel in 1926 was Harold Ambrose Jacques Pittman (1903–81),

[14] https://vwma.org.au/explore/people/161206, viewed May 2023.
[15] Carne (1928).
[16] Samuel and others (1930).
[17] Samuel and others (1930).
[18] Rivett and Lightfoot (1927).
[19] Samuel (1930).
[20] Anonymous (1933).
[21] https://vwma.org.au/explore/units/68/people, viewed May 2023.
[22] Anonymous (1919).
[23] Anonymous (1922). Anonymous (1923).
[24] Osborn and Samuel (1922).

Fig. 3. Geoffrey Samuel (left) and Rupert Best (right) in the laboratory at Waite Institute in January 1934. Rupert Jethro Best—Records 1929–68, Reference PRG 232, State Library of South Australia, Mortlock Library of South Australiana, Adelaide. Photographer unknown.

a University of Sydney graduate with a brilliant academic record, who had been awarded a Silver Medal for his grades.[25]

The relationship between Samuel and Pittman was strained from the beginning because the two had conflicting hypotheses on the vector of the spotted wilt pathogen, with Samuel insisting that it was transmitted by the two-spotted spider mite (*Tetranychus telarius*), whereas Pittman independently pursued a thrips vector hypothesis.[26] When Pittman obtained evidence to support his hypothesis, he rushed into print with a preliminary report suggesting that *Thrips tabaci* was the vector of the spotted wilt pathogen,[27] but there were deficiencies in his experimental design as raised by Samuel and others.[28] Only the thrips used in the last of three transmission experiments were expertly identified by an entomologist. Moreover, the thrips nymphs used in the transmission experiments were directly sourced from plants growing in the grounds of the Waite Institute and from a commercial glasshouse in Adelaide and pure species cultures were never established, therefore raising doubt that all insects used in the experiments were *T. tabaci*. Nevertheless, Pittman provided proof that thrips were transmitting the spotted wilt pathogen, and the conclusion that *T. tabaci* is a vector was independently verified by Kenneth Smith in Great Britain.[29]

According to the history of events recounted by Lionel Stubbs,[30] Pittman's unilateral publication efforts temporarily disrupted relations between the CSIR and the Waite Institute, a claim that is supported by the fact that the CSIR abruptly shifted Pittman to Perth to work on bitter pit of apples with Walter Carne.[31] A serendipitous outcome of this dispute was that in April 1928, Pittman was replaced by John (Jack) Grieve Bald (1905–95) who had a brief but productive partnership with Samuel before departing for England to undertake a PhD at the University of Cambridge in January 1934, probably encouraged and assisted by Samuel, who promoted advanced degree education.[32] After his PhD, Bald had an auspicious career in the Victorian Department of Agriculture and later the University of California Los Angeles and Riverside.

[25]Stubbs (1994). Falvey and Bardsely (1997).
[26]Stubbs (1994).
[27]Pittman (1927).
[28]Samuel and others (1930).
[29]Smith (1931*b*).
[30]Stubbs (1994).
[31]Anonymous (1928).
[32]Krogh (1997).

Controversy dogged Pittman throughout his career, as he was appointed Principal of Dookie Agricultural College in Victoria in 1938 and again his tenure was involuntarily foreshortened. 'His 19 month reign split the College, giving rise to animosities which lasted for decades … he was as stubborn and tactless as they come'.[33] From 1940 to 1968, Pittman was employed as senior plant pathologist at the Plant Research Laboratory Burnley, Victoria, where he overlapped the beginning of Lionel Stubbs' career. Stubbs was equally scathing of Pittman, describing him as having an 'egocentric personality which later resulted in loss of objectivity'.[34] Despite these character flaws, Pittman's colleagues at Burnley did acknowledge that he had a 'prodigious memory and ability to integrate subject matter from a wide range of scientific disciplines when making diagnoses and recommendations on plant health'.[35]

After these initial disputes between the Waite Institute and CSIR were resolved, strong progress was made in elucidating the biology of TSWV within a brief period, culminating in the publication of two classic monographs (CSIR Bulletins). The first monograph authored by Samuel, Bald and Pittman provided the first comprehensive description of the symptomatology of the disease.[36] Preliminary results obtained by Pittman that *T. tabaci* was a virus vector could not be confirmed, although another thrips species, *Frankliniella schultzei* (misidentified as *Frankliniella insularis*) was shown to be an efficient vector and more likely to be the spreader of the disease, as other thrips species that were tested did not 'take kindly' to being force fed on tomatoes.[37] Individual nymphs of *F. schultzei* could acquire the virus after six hours of feeding and retain the pathogen for up to 24 days, through pupation, and following successive transfers to fresh, healthy seedlings on consecutive days. However, the 'infective power' of the thrips did not continue through to the next generation of nymphs, suggesting a lack of transovarial transmission of the virus. The life cycle of *F. schultzei* was described for the first time. Commercial cultivars of tomato were screened for disease resistance, and immunity not found, although cherry tomato was shown to be less susceptible to infection. Inefficient transmission was achieved by rubbing and partly crushing the end leaflets of two leaves with the finger and thumb moistened with the virus, and leaving a drop of virus on the wounded part. Finally, the virus was thrips-transmitted to *Nicotiana glauca*, *Nicotiana suaveolens*, *Nicotiana tabacum*, and *Datura suaveolens*.

The second monograph on TSWV dealt with the adoption and refinement of Holmes' leaf rubbing method of inoculation, host range studies and closer examination of the parameters of thrips transmission.[38] Mechanical transmission rates of 80–100% were achieved by ensuring that a gentle rubbing action was used that did not cause visible wounding and, most importantly, using recently diseased plants as the sources of inoculum. The host range of TSWV was significantly expanded to include other crop plants such as capsicum and aubergine, as well as garden flowers such as nasturtium, Iceland poppy, petunia, aster, and zinnia. Finally, evidence was provided that only nymphs and not adults of *F. schultzei* could acquire the virus. The latter observation was revolutionary and attracted great attention around the world.[39]

In mid-1930, Samuel undertook sabbatical leave for 'few months' at the University of Wisconsin-Madison with Professor James Johnson on an Honorary Fellowship in Plant Pathology, awarded by the Regents of the University of Wisconsin.[40] The purpose of the visit was to test the relative efficiency of Holmes' leaf rubbing method of inoculation compared with the more conventional needle scratching method for six different viruses that were available in Johnson's laboratory, including tobacco mosaic virus (TMV). These studies built on research begun in Adelaide by Bald and himself using TSWV. While in the USA, Samuel took the opportunity to visit Francis Holmes, inventor of the local lesion assay for plant viruses, at the Boyce Thompson Institute in Yonkers, New York, and the two struck up a friendship that was to continue for many years through the frequent exchange of letters.[41]

The final character in the Australian story of the discovery of tomato spotted wilt virus is Rupert Jethro Best (1903–91). Best trained in Physical and Organic Chemistry at the University of Adelaide and after several junior teaching positions at the university, was appointed to the staff of Waite Institute on 1 December 1928 as an assistant chemist to Professor James Prescott.[42]

> During the second half of 1933 Geoffrey Samuel called on me (Best) for advice on some problems they had encountered in the study of Tomato Spotted Wilt (TSW) virus …

[33]Falvey and Bardsely (1997).
[34]Stubbs (1994).
[35]Falvey and Bardsely (1997).
[36]Samuel and others (1930). These authors were the first to to categorise the causal agent of the disease as a virus—tomato spotted wilt virus.
[37]The thrips species that transmitted TSWV in experiments by Samuel and others (1930) was identified by G. D. Morrison from the Imperial Bureau of Entomology as *Frankliniella insularis*, hence this name was adopted throughout the manuscript. However, K. Sakimura from Japan pointed out that this was a misidentification of *Frankliniella schultzei* (cited in Best (1968)) and almost certainly he was correct as *Frankliniella insularis* is yet to be recorded from Australia and *Frankliniella occidentalis*, another major vector of TSWV, was only introduced in 1993 (https://keys.lucidcentral.org/keys/v3/thrips_australia/operating.html, viewed March 2023).
[38]Bald and Samuel (1931).
[39]Best (1968).
[40]Scholthof (2014). Harley (1991) states that Samuel was away from Adelaide for a year, whereas Samuel (1931) says only a few months.
[41]Scholthof (2014).
[42]Best (undated).

I (Best) counselled them to test the relationship between pH values and also redox potentials and to use TMV as a control system … Samuel invited me (Best) to design and conduct experiments … From December 1933 to Easter 1934, Samuel and I (Best) worked seven days a week, day and night.[43]

Three papers arose from this frenetic period of activity (Fig. 3), demonstrating the importance of controlling pH and electrolyte concentration and providing a reducing environment (for example, adding sodium sulfite to the inoculation buffer) to maintain infectivity of the virus.[44] Importantly, Samuel and Best quantified infectivity and validated differences in the inoculation treatments by using the 'half-leaf local lesion assay' developed by Carl Priode.[45] The improvements they made to stabilise the virus in sap extracts had broad implications across the entire spectrum of plant virology research.

In April 1934, Samuel departed Australia to take up a position as a mycologist at Rothamsted Experimental Station in England.[46] There is no doubt that this move was motivated by a desire to escape the academic isolation and poor experimental facilities that he encountered in Adelaide. In a letter to Francis Holmes in 1932, he complained: 'The main disadvantages are in the matter of greenhouse accommodation, which is fair but practically unheated, and in the isolation so that one never meets anyone to argue with'.[47] He later stated: 'I have taken the post of mycologist at Rothamsted, in order to get more into the centre of things for a few years'.[48]

Samuel's ambitions were not fulfilled at Rothamsted, as communicated to Rupert Best:

Since I have arrived here I have "felt" that I am expected to be entirely mycological. In fact I haven't much more than the remotest idea after 2 months what the virus people are doing … what makes me tear my brain most, almost shriek, is that the 4 members of the virus team are each working independently … and they don't know what each are doing … They are still even jabbing plants with needles … it is a relief to be able to explode in some direction … He (Caldwell) is the most self-opinionated ass I have ever met who won't discuss a single thing – merely slings mud at all the virus workers in the world. You'd think that one of them would be ready to discuss viruses with you – but no! dead secrets![49]

Ironically, Professor John (Jack) Harley, mycologist at Oxford University, described Rothamsted at the time of Samuel's employment as being 'a small, well-knit, friendly place'.[50] Samuel could have been a victim of an arrogant and aloof attitude that some English gentlemen had towards colonial Australians. He reserved his kindest words for Marion (Hamilton) Watson, the sole female scientist in the virology team, who worked on aphid transmission of viruses and likely suffered prejudice in a separate way.

Samuel left Rothamsted in 1937 but remained in Great Britain to become a mycologist (plant pathologist from 1944) at the Ministry of Agriculture's Plant Pathology Laboratory.[51] In 1948 he was transferred to the Agricultural Research Council to organise their potato work and subsequently took charge of the Entomology and Mycology Division as Scientific Assistant to the Secretary of Agriculture—a post he held until his retirement in 1962. After leaving Australia, he never again did plant virological research judging by his publication record. In contrast, Best remained a plant virologist at the Waite Institute and worked alone on TMV and TSWV, producing several classic papers on them.

To this day, TSWV is still regarded as a difficult virus to work with due to the lability of the virions, problems with transmission and challenges associated with raising laboratory cultures of thrips. What makes the work of Samuel and his colleagues even more remarkable is that it was performed during the Great Depression, when economic conditions were the harshest to be experienced in the twentieth century. Electron microscopy, which allows direct observation of virions, was also unheard of at the time.

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[43] Best (1977).
[44] Best and Samuel (1936*a*, 1936*b*). Samuel and others (1935).
[45] Priode (1928).
[46] Anonymous (1934).
[47] Samuel (1932).
[48] Samuel (1933).
[49] Samuel (1934).
[50] The work culture at Rothamsted is mentioned by Harley (1991) in his obituary for Stephen Denis Garrett. Samuel and Garrett worked together at Rothamsted for a brief period before the former left to join the Ministry of Agriculture. Earlier in his career (1929–33), Garrett had been employed as an assistant to Samuel at Waite Institute, working on the 'Take-all' and 'No-growth' diseases of cereals, but eventually returned to Great Britain. Garrett began a lifelong friendship with Jack Bald during his time in Australia.
[51] Ainsworth (1996).

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