SPECIAL ISSUE | HISTORICAL ARTICLE
https://doi.org/10.1071/HR23020

Historical Records of Australian Science

'From Snowy River, up by Kosciusko's side': a virus, a beetle, and a PhD

P. L. Guy[A,*]

For full list of author affiliations and declarations see end of paper

*Correspondence to:
P. L. Guy
Department of Botany, University of Otago, Dunedin, New Zealand
Email: paul.guy@otago.ac.nz

Published: 18 March 2024

Cite this: Guy, P. L. (2024) 'From Snowy River, up by Kosciusko's side': a virus, a beetle, and a PhD. *Historical Records of Australian Science*, doi:10.1071/HR23020

ABSTRACT

A chance discovery early in 1980 led to a body of work on a virus and a rare species that lasted until the end of the decade. The discovery and characterisation of turnip yellow mosaic virus (TYMV-Cd) infecting one-fifth of the fragmented population of *Cardamine robusta* at Mt Kosciuszko, New South Wales, revealed a puzzle that remains unresolved. There is no clear explanation as to why there is a population of TYMV here in the Southern Hemisphere whose sequence has only diverged from Northern Hemisphere TYMV by a few percent. Adding to the mystery is the fact that TYMV-Cd only infects one of the rarest and geographically most restricted species in Australia, while it is surrounded by potential hosts known to be infected in the Northern Hemisphere. This article reviews research published on TYMV at Mt Kosciuszko during the 1980s and 1990s. While human agency cannot be ruled out, indications are that TYMV established without human intervention. The work is set in a historical context and highlights some of the changes around how plant virology is done.

Keywords: beetle taxonomy, botany, cardamine, history of science, plant pathology, scientific method, tymovirus, viruses.

Introduction

A camping holiday on the Australia Day long weekend 1980 revealed a scientific puzzle that remains unresolved. *Cardamine robusta* (Brassicaceae: *syn C. lilacina*) large sward-forming variant,[1] is one of the rarest (thankfully not threatened) species in Australia, restricted to a few picturesque tarns and rocky slopes high in the Kosciuszko National Park, New South Wales, south-eastern Australia.[2] It grows in a UNESCO World Heritage Region on sites near late snow-patches on the margins of streams and lakes in the Kosciuszko alpine area and approximately 20% of the swards display a bright yellow mosaic pattern on their leaves caused by turnip yellow mosaic virus (TYMV-Cd) infection. Like general botanical fieldwork, much plant virology fieldwork used to be done on family holidays and on refuelling and toilet breaks at the roadside, with no safety plan or risk assessment, just a pile of receipts, and a log book. I spent the first year of my doctorate, 1979, searching for viruses in the Australian flora mainly focussed on eucalypts which was hard going and yielded almost nothing I could work with. My first collection of cardamine was made on a hike with two colleagues through the headwaters of the Snowy River and over a ridge to Lake Albina. From a campsite by Lake Albina we climbed toward Mt Townsend,[3] 'up by Kosciusko's side',[4] and I stowed a promising-looking plant safely in a plastic bag with an uneaten sandwich, forgotten about, and left in a ruck sack for a week before it was examined.

[1]Costin and others (1979, 2000). Thompson and Ladiges (1996).
[2]Spelling changed from Kosciusko in 1997 in line with the original Polish name: 'Kosciuszko'. Geographical Names Register (GNR) of NSW. Geographical Names Board of New South Wales.
[3]Quite literally: early Victorian maps mislabel Mt Townsend as Mt Kosciusko.
[4]Patterson (1895). Quoted from the poem 'The man from Snowy River', verse 5 line 1.

A virus

Symptomatic leaves were photographed (Fig. 1), ground in water and mechanically inoculated to Chinese cabbage seedlings, the brassica of choice for experimental work at the time.[5] Arabidopsis was not used back then. Other sap extracts were mixed with phosphotungstate and observed on formvar coated grids in the transmission electron microscope (TEM). The first field of view on the first grid displayed hundreds of virus particles: 28 nm spheres some showing a little surface detail some penetrated by the stain (Fig. 2). Early indications were that this was a tymovirus, a group of viruses that my supervisor Adrian Gibbs and the Virus Ecology Research Group at the Research School of Biological Sciences (ANU) knew well. Confirmation took longer in the absence of instant screen shots, the phosphor screen in the TEM had to be swung out of the way, a 120 × 85 mm black and white film negative was exposed, then developed, checked and finally printed maybe a week later. Meanwhile, over the course of the same week or so the Chinese cabbage seedlings began developing a bright yellow vein clearing and then mosaic typical of turnip yellow mosaic virus infection.[6] This first isolate was named the RR-isolate after my two companions on that first trip, Robyn Overall and Rosemary White, who became senior scientists at the University of Sydney and CSIRO, respectively.

Serological testing showed that the virus was closely related to the original TYMV from Europe. Enzyme linked immunosorbent assays (ELISA) were in their infancy,[7] and rapid antigen testing was well over the horizon so Ouchterlony double immunodiffusion tests were used to work out the virus's relationships.[8] Strong precipitin bands formed when virus particles diffused towards wells containing antibodies developed to TYMV and weaker bands developed when the virus interacted with antibodies to some other tymoviruses. Antisera and purified antibodies were

Fig. 1. A leaf of *Cardamine robusta* showing symptoms caused by the RR-isolate of TYMV-Cd. Reproduced from Guy and Gibbs (1981). Original is a 35 mm slide taken by P. L. Guy, 1980.

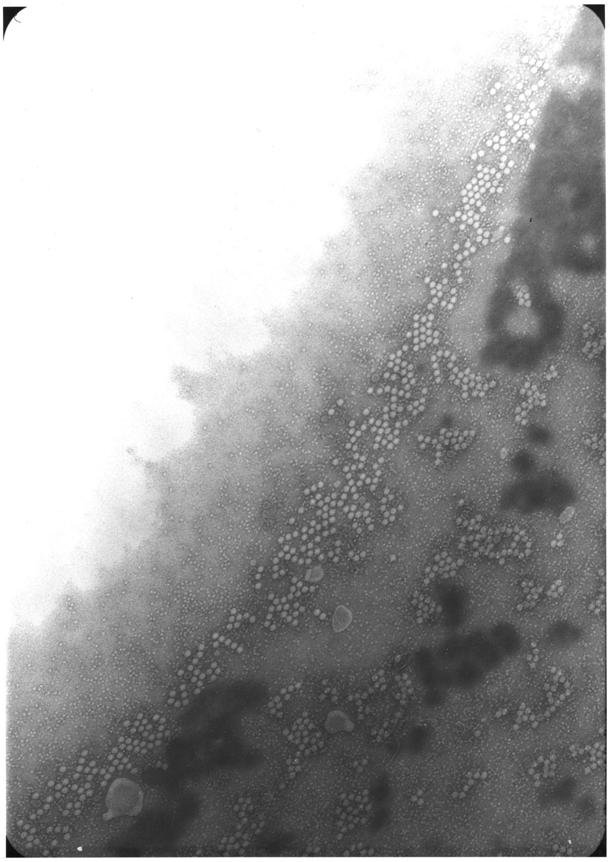

Fig. 2. One of the first transmission electron microscope images of TYMV particles (33 000× magnification) from Kosciuszko. Photo by P. L. Guy, 1980.

[5]Kado and Agrawal (1972).
[6]Broadbent and Heathcote (1958).
[7]Clark (1981).
[8]Wilson (2014).

not generally available and researchers made their own collections by writing letters to colleagues and hoping small packets with antisera would eventually arrive in the mail. James Dale at the Department of Primary Industry at Indooropilly, Brisbane hosted me for a few days while I ran my virus isolates against his collection of antisera. The virus was easily purified and large amounts of RNA were extracted and used in the dideoxynucleotide chain termination method with polyacrylamide gel electrophoresis and autoradiographed at −70°C, then the sequence was manually read from X-ray film. This produced sequences of up to 200 bases, a modest achievement these days but a solid amount of work in the 1980s. Further comparisons were made using cDNA-RNA hybridisation tests and by analysing fragments produced from cDNA-RNA hybrids by restriction endonucleases.[9]

All the results showed there were only small differences between the TYMV-Cd isolates from Kosciuszko and a group of isolates from Europe (TYMV-1), more than 16 000 km away. They differed by approximately 1% and biogeographic evidence suggested that the populations separated more than 12 000 years ago. TYMV-2 isolates from Europe differed from TYMV-1 and the Kosciuszko isolates by 5–11%.[10]

A beetle

On a field trip by Adrian Gibbs to Blue Lake, in the Kosciuszko National Park, cardamine was located on the eastern facing rocky shore. Many of the swards displayed the bright yellow mosaic pattern seen at Lake Albina. The most exciting find of the day was a tiny, red, pill-beetle found resting deep down on the fleshy decumbent stems.[11] Tymoviruses are transmitted by beetles and this was a prime candidate. We visited John Lawrence at CSIRO Entomology who initially poured cold water on this idea. He determined the beetle to be a species of *Pedilophorus*, a byrrhid known to feed on mosses and other bryophytes like the ones twining through the cardamine swards. The beetle fed happily on cardamine in the laboratory, and after feeding on infected leaves was placed on Chinese cabbage seedlings, and successfully transmitted the virus. Beetles are known to feed on a number of substrates in the laboratory so this result was not convincing. Fresh collections of the beetles from infected swards at Blue Lake proved that the beetles transmitted the virus.[12] Beetle extracts used in immune serum electron microscopy revealed that the beetles ingested infected cardamine. Thus plant virology was used to establish that this byrrhid, from a family usually associated with bryophagy, was feeding on a dicotyledonous plant. When the Australian byrrhids were revised this was acknowledged; the beetle was moved to a different genus and given the epithet *Notolioon cardamine*.[13] There were still reservations about the beetle's ability to be an effective vector in the field. The beetle's elytra were fused,[14] so no wings and no prospect of flying between swards that were often ten metres apart through a tangle of alpine grasses. In the laboratory the beetle seemed quite sedentary. The field season at Kosciuszko was always short: by late April snow was beginning to cover the swards and they, generally, did not re-emerge from the melting snow until mid-November. The weather was unpredictable, so spur-of-the-moment trips led to making the most of good weather and leaving the high country at sunset. All doubts about the beetle's capacity to transmit the virus between swards were dispelled on a late-night return to Canberra. As a styrofoam Eskie was opened a wave of beetles lapped over the rim and made a run for it across the lab bench: the beetle was nocturnal!

Other beetle vectors of other tymoviruses discriminate between healthy and infected host plants: showing a preference for infected plants. This is because infected plants have a higher polyamine content than uninfected controls. The Kosciuszko beetles did not discriminate and there appeared to be no difference in the taste between infected and uninfected plants, although I did discover why the common name for cardamine is bitter cress.

Each day trip involved a two-hour drive to Charlotte Pass followed by a two-to-hree-hour walk to each site. To improve my efficiency, on 17 December 1980 I decided to set up camp at the Lake Albina hut for two days of field work. No sooner had I set out my field gear than a blizzard set in and snow fell for the rest of the day and into the night. Next day there was just under a metre of snow on the ground and it was clear no work would be done. Further hut stays and camps were much more productive than this first one.

A long search

Rosette-forming species of cardamine that grew near the infected swards always appeared healthy, although they were susceptible to the virus after inoculation in a glasshouse. Similarly, cardamines from a lower altitude were always healthy, but susceptible to TYMV.[15] Samples of

[9]Blok and others (1987). Keese and others (1989). Hayden and others (1998).
[10]Gibbs and others (1986).
[11]Guy and Gibbs (1981). Gibbs and others (1986).
[12]Guy and Gibbs (1985).
[13]Lawrence and Britton (1994). Lawrence and others (2013).
[14]Gibbs and others (1986).
[15]Guy and Gibbs (1981).

Cardamine gunnii taken by colleagues from Mt Cobberas in Victoria were also free of TYMV.[16] The beetles were never found on these species. Ten years' sampling cardamines in Tasmania revealed no infected plants. *Cardamine robusta* and the beetle have not been reported from Tasmania but the rare brassica *Pachycladon radicata* (formerly *Cheesmania radicata*) occupies a similar niche forming small swards in boulder screes watered by late snowbanks. Pachycladon and the Tasmanian cardamines were susceptible to TYMV in glasshouse tests but they were not infected in the field. However, these populations were invaded by turnip yellows virus (formerly designated as beet western yellows virus).[17] Thirty years' sampling cardamine in New Zealand, including a trip to sub-Antarctic Campbell Island, has failed to find TYMV, but again, some of the native *Pachycladon* species have been invaded by other viruses.[18] While the wider search for TYMV in cardamine has been fruitless, weekend expeditions formed the framework for other studies particularly in the search for viruses invading the grass floras of the region.[19]

Eurasia is hypothesised as the evolutionary origin of *Cardamine*.[20] There is a high diversity of species in the region. The genus rapidly colonised and diversified across the Northern Hemisphere. Native and endemic species of *Cardamine* occur almost everywhere except Antarctica,[21] although they occur on many of the isolated sub-Antarctic islands and some have their own endemic species.[22] The group spread across the globe to the Southern Hemisphere as several closely related lineages.[23] One example of very long-distance dispersal followed by rapid speciation is provided by the Australian and New Zealand taxa, which form a monophyletic group together with one from the Bering Strait and one from South America.[24]

The Australian Virtual Herbarium and the Global Biodiversity Information Facility show that there are alpine species in Papua, Sulawesi and the Philippines that have not been investigated for virus infection and may provide shorter bridging distances than those inferred by the relationship between Bering Strait and Australian and New Zealand species of cardamine.

TYMV infects wild and cultivated brassicas in Europe, North-East Asia and North America but is so far only reported from the rare endemic *C. robusta* from Australia in the Southern Hemisphere. One possible means of introduction to the Southern Hemisphere is via infected seed transmission. TYMV is seed transmitted in some of its Northern Hemisphere hosts. TYMV was seed transmitted in *Brassica napus* (2–8%) in central Europe and in *Brassica pekinensis* (2%) in Spain and Japan.[25] Only small numbers of seeds from infected cardamine were ever tested but nearly 3% (2/70) of seedlings germinated from infected *Cardamine* sp A plants were infected.[26]

Another field trip to Blue Lake at Kosciuszko revealed that another pathogen of cardamine had made the trans-hemispheric journey. Pustules caused by the microcyclic rust *Puccinia cruciferarum* were conspicuous on the underside of leaves of some of the swards. This was the first record of a rust of brassicas in Australia.[27] Unlike TYMV's limited incursion into the Southern Hemisphere, *P. cruciferarum* also infects cardamines in New Zealand and Chile. Furthermore, it has diverged into distinct subspecies at Kosciuszko and New Zealand (subsp. *inornata*) and Chile (subsp. *cardamines-cordatae*). Microcyclic rusts are not known for long distance dispersal and it is believed that *Puccinia* would have spread with its hosts to the Southern Hemisphere.[28]

Pollen and radiocarbon analyses of cores from Blue Lake, Club Lake and Pounds Creek in Twynam Cirque record change back to the end of the Last Glacial approximately 13 000 years ago. Cardamine pollen was plentiful in samples from 12 000 to 8000 years ago.[29] The tree line was probably lower down the mountain. This suggests that cardamine populations may have been larger and more contiguous before dryer conditions saw them retreat to the isolated refuges they occupy today.

Brassicas were present in southeast Australia before the Last Glacial. Their pollen has been found in samples dating between 35 000 and 18 000 years ago in cores from the bed of Lake George, New South Wales. The oldest record of brassica pollen in Australia is from the bottom sample of a core from Pulbeena Swamp in northwest Tasmania dated at 65 000 years ago.[30]

[16]Guy and Gibbs (1985).
[17]Guy (1987). Guy (1998).
[18]Fletcher and others (2010).
[19]For example Guy (1991). Davis and Guy (2001). Delmiglio and others (2010).
[20]Carlsen and others (2009).
[21]Al-Shehbaz and others (2006).
[22]Heenan (2008).
[23]Bleeker and others (2002). Carlsen and others (2009). Mitchell and Heenan (2000). Heenan (2017).
[24]Carlsen and others (2009).
[25]Alfaro-Fernandez and others (2016). Kirino and others (2008). Špak and others (1993). Stobbs and others (1998).
[26]Guy (1982).
[27]Gibbs and others (1986).
[28]Walker (1996).
[29]Martin (1986).
[30]Colhoun and others (1982).

A PhD: thesis and manuscript writing

Before online searches, literature searches involved regular visits to the library and looking at paper copies of the latest journals to grace the shelves. Newly received issues were all placed on the shelves together once a week, which gave it a sense of occasion. Abstracts were collated and printed on fine tissue-like paper: Current Contents, and CAB International Review of Plant Pathology, the latter including abstracts of papers under various subject headings and useful reviews.

Computer searches were very basic. Doctoral students sent search terms to Lockheed in the United States and a couple of weeks later a printout arrived in the mail. In those days most of us were still search-and-stab typists so thesis and paper drafts were written by hand usually double-spaced on note paper and cut and pasting was literally done with scissors and sticky tape or glue. In the late 1970s electric typewriters were replacing the traditional finger driven ones which gave the final product a much more professional appearance. There were still pools of typists in offices and some of these earned themselves extra cash typing theses for those of us who had not learned to type. These were the days of early personal computing and only the most devoted early-adopters ventured into the realm. Typical tea room conversations went along the lines: 'I tried all night and I almost printed a page with my dot matrix printer'. The quote for my thesis was $1.00 per page using Courier, the font of the day. If I wanted to use italics for species names there would be a 10 cent charge for each change of the golf ball that delivered the typeface to the ribbon. A quick calculation showed that many pages would cost me triple so I settled for the binomials being underlined: no extra charge. These typewriters had no memory so any small errors could be corrected with white-out otherwise the whole page had to be retyped. The research school's director's office had one of the early IBM machines with memory; it was the size of a chest freezer! Graphs and other figures were produced using tracing paper and Rotring ink pens. Text and symbols were produced using the Headliner, Dymo or Letraset systems and then the transfers were carefully applied to the tracing paper. There was often a person in your building who was skilled in the art of retouching photographs. They used a grey-scale series of watercolour paints and a very fine paint brush to blend out imperfections such as dust, fibres or scratches from your black and white prints. The final figure was photocopied or photographed and printed before binding. Manuscripts were produced by more cutting and pasting and adapting to a journal's format. The cover letter was typed up and sealed in a manila envelope with three hard copies of your manuscript. My favourite part of the submission process was taking it to a post office, licking the stamps and sending it down the chute. Much more satisfying than hitting the submit button on a computer.

Conclusions

Although the way we do science has changed, the puzzle about the origin of the turnip yellow mosaic virus on *Cardamine robusta* at Mt Kosciusko remains. After forty years of searching, this is still the only recorded site of TYMV in the Southern Hemisphere (Geering and Thomas 2022). This is despite the fact that healthy *C. lilacina* plants grow within metres of infected swards and susceptible brassica weeds and crops grow all over south-east Australia and beyond. Modern genomics and phylogenetic techniques are needed to give new perspective on the enigma. Although the virus's journey to Kosciuszko is still unclear, and human agency cannot be ruled out, long-distance dispersal is no longer as fanciful a notion as it was in the 1980s. Sea bird migrations from the Bering Strait to southern New Zealand, for example, are measured in days. Other species of forest and wetlands birds do annual migrations between Australia and New Zealand and Papua New Guinea and South-East Asia. Alpine Islands containing potential hosts are dotted along these routes. Investigation of these areas may provide additional pieces to the puzzle.

References

Alfaro-Fernandez, A., Serrano, A., Tornos, T., del Carmen Cebrián, M., del Carmen Córdoba-Sellés, M., Jordá, C., and Font, M. I. (2016) *Turnip yellow mosaic virus* in Chinese cabbage in Spain: commercial seed transmission and molecular characterisation, *European Journal of Plant Pathology*, **146**, 433–442. doi:10.1007/s10658-016-0929-3

Al-Shehbaz, I. A., Beilstein, M. A., and Kellogg, E. A. (2006) Systematics and phylogeny of the Brassicaeae (Cruciferae): an overview, *Plant Systematics and Evolution*, **259**, 89–120.

Bleeker, W., Franzke, A., Pollmann, K., Brown, A. H. D., and Hurka, H. (2002) Phylogeny and biogeography of Southern Hemisphere high-mountain Cardamine species (Brassicaceae), *Australian Systematic Botany*, **15**, 575–581.

Blok, J., MacKenzie, A., Guy, P., and Gibbs, A. (1987) Nucleotide sequence comparisons of turnip yellow mosaic virus isolates from Australia and Europe, *Archives of Virology*, **97**, 283–295. doi:10.1007/BF01314427

Broadbent, L., and Heathcote, G. D. (1958) Properties and host range of turnip crinkle, rosette and yellow mosaic viruses, *Annals of Applied Biology*, **46**, 585–592. doi:10.1111/j.1744-7348.1958.tb02242.x

Clark, M. F. (1981) Immunosorbent assays in plant pathology, *Annual Review of Phytopathology*, **19**, 83–106. doi:10.1146/annurev.py.19.090181.000503

Carlsen, T., Bleeker, W., Hurka, H., Elven, R., and Brochmann, C. (2009) Biogeography and Phylogeny of *Cardamine* (Brassicaceae), *Annals of the Missouri Botanical Garden*, **96**(2), 215–236. doi:10.3417/2007047

Colhoun, E. A., van de Geer, G., and Mook, W. G. (1982) Stratigraphy, pollen analysis and paleoclimatic interpretation of Pulbeena Swamp, Northwestern Tasmania, *Quaternary Research*, **18**, 108–126. doi:10.1016/0033-5894(82)90024-2

Costin, A. B., Gray, M., Totterdell, C. J., and Wimbush, D. J. (1979) *Kosciusko Alpine Flora*, 1st edn, CSIRO/Collins Publishing, Sydney, Australia.

Costin, A. B., Gray, M., Totterdell, C. J., and Wimbush, D. J. (2000) Kosciuszko Alpine Flora, 2st edn, CSIRO Publishing, Collingwood, Vic.

Delmiglio, C., Pearson, M. N., Lister, R. A., and Guy, P. L. (2010) Incidence of cereal and pasture viruses in New Zealand's native grasses, *Annals of Applied Biology*, **157**, 25–36. doi:10.1111/j.1744-7348.2010.00406.x

Davis, L. T., and Guy, P. L. (2001) Introduced plant viruses and the invasion of a native grass flora, *Biological Invasions*, **3**(1), 89–95. doi:10.1023/a:1011464804245

Fletcher, J. D., Lister, R. A., Bulman, S. R., and Heenan, P. B. (2010) First record of *Turnip mosaic virus* in *Pachycladon* spp. (Brassicaceae): an endangered native plant species in New Zealand, *Australasian Plant Disease Notes*, **5**, 9–10. doi:10.1071/DN10004

Geering, A. D. W., and Thomas, J. E. (2022) An updated register of viruses and viroids that infect ornamental, turf and native plant species in Australia, *Australasian Plant Pathology*, **51**, 135–139. doi:10.1007/s13313-021-00849-2

Gibbs, A. J., Blok, J., Coates, D. J., Guy, P. L., Mackenzie, A., and Pigram, N. (1986) 'Turnip yellow mosaic virus in an endemic Australian alpine *Cardamine*' in *Flora and Fauna of Alpine Australasia: Ages and Origins*, ed. B. A. Barlow, CSIRO, Melbourne, pp. 289–299.

Guy, P. L. (1982) Viruses, host range, and the Australian flora, PhD thesis, Australian National University, Canberra.

Guy, P. L. (1987) Beet western yellow virus infection of *Cardamine* Spp. and *Cheesemania radicata*, *Australasian Plant Pathology*, **16**, 43–44. doi:10.1071/APP9870043

Guy, P. L. (1991) Barley yellow dwarf virus infection of the Gramineae in Tasmania, *Acta Phytopathologica et Entomologica Hungarica*, **26**, 21–27.

Guy, P. L. (1998) 'Survey of fungal endophytes and brassica viruses', in *Wilderness Ecosystems Baseline Studies (WEBS): Pelion Plains-Mt Ossa*, eds M. M. Driessen, M. D. Comfort, J. Jackson, J. Balmer, A. M. M. Richardson, P. B. McQuillan, Tasmanian Parks and Wildlife Service Wildlife Report, 98/2, pp. 43–45.

Guy, P., and Gibbs, A. (1981) A tymovirus of *Cardamine* sp. from alpine Australia, *Australasian Plant Pathology*, **10**, 12–13. doi:10.1071/APP9810012

Guy, P. L., and Gibbs, A. J. (1985) Further studies on turnip yellow mosaic tymovirus isolates from an endemic Australian *Cardamine*, *Plant Pathology*, **34**, 532–544. doi:10.1111/j.1365-3059.1985.tb01404.x

Hayden, C. M., Mackenzie, A. M., and Gibbs, A. J. (1998) Virion protein sequence variation among Australian isolates of turnip yellow mosaic tymovirus, *Archives of Virology*, **143**, 191–201. doi:10.1007/s007050050279

Heenan, P. B. (2008) *Cardamine latior* (Brassicaceae), a new species endemic to the subantarctic Auckland Islands, New Zealand, *New Zealand Journal of Botany*, **46**, 559–566. doi:10.1080/00288250809509785

Heenan, P. B. (2017) A taxonomic revision of *Cardamine* L. (Brassicaceae) in New Zealand, *Phytotaxa*, **330**, 1–154. doi:10.11646/phytotaxa.330.1.1

Kado, C. I. and Agrawal, H. O. (1972) *Principles and Techniques in Plant Virology*, Van Nostrand Reinhold Co, New York.

Keese, P., Mackenzie, A., and Gibbs, A. (1989) Nucleotide sequence of the genome of an Australian isolate of turnip yellow mosaic tymovirus, *Virology*, **172**, 536–546. doi:10.1016/0042-6822(89)90196-7

Kirino, N., Inoue, K., Tanina, K., Yamazaki, Y., and Ohki, S. T. (2008) *Turnip yellow mosaic virus* isolated from Chinese cabbage in Japan, *Journal of General Plant Pathology*, **74**, 331–334. doi:10.1007/s10327-008-0108-2

Lawrence J. F and Britton E. B. (1994) *Australian Beetles*, Melbourne University Press, Melbourne.

Lawrence, J. F., Slipinski, A., Jäger, O., and Pütz, A. (2013) The Australian Byrrhinae (Coleoptera: Byrrhidae) with descriptions of new genera and species, *Zootaxa*, **3745**, 301–329. doi:10.11646/zootaxa.3745.3.1

Martin, A. R. H. (1986) 'Late glacial and early Holocene vegetation of the alpine zone Kosciusko National Park', in *Flora and Fauna of Alpine Australasia: Ages and Origins*, ed. B. A. Barlow, CSIRO, Melbourne, pp. 161–170.

Mitchell, A. D., and Heenan, P. B. (2000) Systematic relationships of New Zealand endemic Brassicaceae inferred from nrDNA ITS sequence data, *Systematic Botany*, **28**, 95–105.

Patterson, A. B. (1895) *The Man from Snowy River and other Verses*, Angus and Robertson, Sydney.

Stobbs, L. W., Cerkauskas, R. F., Lowery, T., and VanDriel, L. (1998) Occurrence of turnip yellow mosaic virus on oriental cruciferous vegetables in Southern Ontario, Canada, *Plant Disease*, **82**, 351. doi:10.1094/PDIS.1998.82.3.351A

Thompson, I. R., and Ladiges, P. Y. (1996) A revision of the *Cardamine gunnii-lilacina* complex (Brassicaceae), *Muelleria*, **9**, 145–159. doi:10.5962/p.198444

Walker, J. (1996) 'The rusts of Cardamine-the geography of genes', in *Fungi of Australia*, vol. 1A, CSIRO Publishing, Melbourne, pp. 279–284.

Wilson, C. R. (2014) *Applied Plant Virology*, CABI, Wallingford, UK.

Špak, J., Kubelková, D., and Hnilička, E. (1993) Seed transmission of turnip yellow mosaic virus in winter turnip and winter oilseed rapes, *Annals of Applied Biology*, **123**, 33–35. doi:10.1111/j.1744-7348.1993.tb04069.x

Data availability. Not applicable, all data cited has been previously published.

Conflicts of interest. There is no conflict of interest.

Declaration of funding. This research did not receive any specific funding.

Acknowledgements. Thanks to colleagues and friends for their assistance in the field and for leaping into alpine tarns with me on hot summer days.

Author affiliation

[A]Department of Botany, University of Otago, Dunedin, New Zealand.