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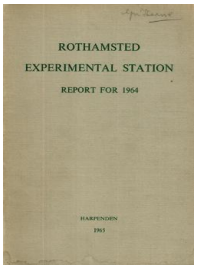

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THE POTATO VARIETY KING EDWARD VII AND PARACRINKLE VIRUS

F. C. BAWDEN and B. KASSANIS

The story of potato paracrinkle virus is worth telling for several reasons in addition to its intrinsic interest. It illustrates, as well as any other, both the extent to which knowledge about the behaviour of viruses has grown during the past 30 or so years and the unsuspected complexity of this behaviour. Perhaps better than most, it shows how practical problems can produce subjects for academic research and how in turn this research can benefit practice. It also provides a valuable cautionary tale, showing that science is not free from its myths, and that, although these mainly arise when speculation outstrips facts, what is factual is often far from sure. Most of the features of paracrinkle virus generally accepted in the 1930s as established have since been proved to be untrue.

The discovery of paracrinkle virus. Paracrinkle virus was discovered at the Potato Virus Research Station, Cambridge, where in the late 1920s Dr. R. N. Salaman was engaged in the practical task of increasing the yield of the commonly grown potato varieties. His aim was to replace the diseased stocks then in use with healthy ones and, as a first step, he was seeking virus-free plants, whose progeny could then be bulked and put into commerce. His method was to select vigorous plants growing in the best potato "seed-growing" districts, take tubers from them to plant in glasshouses at Cambridge, where the foliage was critically examined for symptoms and the plants were further tested by grafting scions from them on to indicator potato varieties and inoculating their sap to potato and to other species, such as tobacco (*Nicotiana tabacum*) and *Datura stramonium*.

The common virus diseases then recognised were leaf roll, crinkle, severe mosaic and mild mosaic, of which crinkle is caused by the joint action of two viruses later identified and named potato A and X, severe mosaic by virus Y and mild mosaic by virus X. It proved easier to get plants of the variety King Edward VII free from these viruses than of most other varieties, because these viruses all produce evident symptoms in King Edward, and virus X, which was then almost universal in many varieties, kills King Edward plants. Nevertheless, it proved impossible to find a virus-free King Edward plant, for scions from every one tested, however vigorous, when grafted to the variety Arran Victory caused a crippling disease, which Salaman and Le Pelley (1930) called paracrinkle. The symptoms, especially of plants in their second and later years of infection, differed from any previously described. Although individual plants differed somewhat in the severity of their reaction, a fact that Salaman (1932) wrongly attributed to a variable association between paracrinkle virus and virus Y, characteristically the young shoots of grafted Arran

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Victory plants first developed bright yellow blotches on their upper leaves, which also became severely waved and crinkled. Plants grown from the tubers of infected plants were mostly miserable, reaching only a few inches high, with shortened internodes and grossly deformed leaves, a condition aptly described as curly dwarf. Some varieties other than Arran Victory also developed severe symptoms when infected by grafting, but some were little affected, and the variety President looked normal.

Salaman and Le Pelley failed to infect other potato varieties or other plant species by inoculating them with sap from King Edward and also failed to transmit paracrinkle virus with the aphid *Myzus persicae*. Other features also seemed to suggest that the virus had no vector. For example, although King Edward was the second most widely grown potato variety in England, and so each year there were vast numbers of plants providing potential sources of infection, paracrinkle was never reported occurring naturally in plants of varieties that show the disease when infected by grafting; also, with King Edward and Arran Victory planted alternately in rows at Cambridge, tubers saved from the Arran Victory plants, although often infected with leaf roll or virus Y, were never infected with paracrinkle virus.

Various other workers confirmed that grafting Arran Victory with scions from King Edward plants always produced paracrinkle, and it became increasingly likely that the virus was present in the whole clone, although this was obviously impossible to prove. These other workers discovered nothing to conflict with the conclusion of Salaman and Le Pelley that King Edward was the "perfect carrier" and unharmed by the virus, which seemed distinct from any other and to be only of academic interest because it had no natural method of spread into plants it could harm.

Paracrinkle virus and plasmagenes. Little research was done on paracrinkle virus for some years, and perhaps little more would have been done had the virus not become a prime subject for speculation in discussions on the origin of viruses. The isolation in the 1930s of several viruses as nucleoproteins suggested that their nearest analogues might be normal nucleoproteins rather than the pathogenic micro-organisms to which most workers had previously related them. In turn this suggested a possible origin of viruses either in faulty synthesis during normal nucleoprotein metabolism or by the accident that a nucleoprotein of one type of organism might get introduced into another where it could multiply and be pathogenic.

Bawden (1939) pointed out that there seemed two equally plausible explanations of what was then accepted knowledge about paracrinkle virus: (1) that the original King Edward seedling became infected with a virus that had since lost its natural method of spread and been perpetuated only by the vegetative propagation of its host; (2) that it was a normal component of King Edward transmissible by grafting to other potatoes, in some of which it was pathogenic. He stressed the uncertainties of any interpretation and that nothing was known about the early history of the variety, but the idea that the virus was intrinsic to King Edward was

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accepted by some writers as though it were established (Darlington, 1944; 1949; Plank, 1948). Paracrinkle virus was advanced as evidence both that viruses derive from plasmagenes, the postulated entities responsible for characters inherited through the cytoplasm, and that a cell protein beneficial in one genotype could be destructive in another. Darlington (1949) separated it off from other viruses in a group he called "provirus", distinguished by being transmissible only by grafting and becoming a virus when introduced by grafting into another genotype.

As the parents of the King Edward variety are unknown, the same cross could not be repeated to see whether it would re-create the virus. (According to Salaman (1926) the original seedling was bred by a gardener in Northumberland, who called it Fellside Hero, and after passing from him to a farmer in Snaith, Yorkshire, it reached J. Butler, who multiplied the stock and marketed it in 1902 under the name King Edward VII.) Also, King Edward plants rarely flower, so the inheritance of the virus is difficult to study, but differences from the expected behaviour of a plasmagene were evident in the fact that none of 22 seedlings from seed set by King Edward pollinated from the variety Flourball contained paracrinkle virus (Carson, Howard, Markham and Smith, 1944).

The postulate that paracrinkle virus arises as a consequence of grafting was invalidated when paracrinkle was produced by inoculating Arran Victory plants with sap from King Edward. Salaman and Le Pelley (1930) failed to do this because their method of inoculation (scratching leaves with a needle through a drop of sap) was inadequate. When leaves of Arran Victory plants were dusted with a diatomaceous earth or carborundum powder and then rubbed with sap from King Edward some developed paracrinkle, and the proportion that did increased when the Arran Victory plants were kept in darkness for a few days before they were inoculated (Bawden, Kassanis and Nixon, 1950). These methods of inoculation and treatment of plants also increase the ease with which many other viruses are transmitted by inoculation. Had Salaman and Le Pelley inoculated sap to tomato (*Lycopersicum esculentum*) instead of to tobacco and *Datura stramonium*, they might well have discovered its transmissibility, for whereas the two plants they used are immune to the virus, tomato is much more susceptible to infection than potato, and their method is adequate to infect this host. However, they might still have failed to do so, for infected tomato plants show no evident effects on their foliage or growth, and the infection would have remained undetected unless they had grafted scions from the tomato plants to Arran Victory plants.

The transmission by inoculation to tomato gave the first information about the particles of paracrinkle virus and allowed some of its properties to be studied. Infected tomato plants contained specific particles about 10 mμ wide and of various lengths, resembling some other viruses both morphologically and in their susceptibility to destruction by heating. Sap from King Edward plants and plants of Arran Victory with paracrinkle, whether infected by grafting or inoculation, also contained elongated particles, but the identity of these was uncertain, because supposedly virus-free plants of Arran Victory and of some other potato varieties, including some recently bred seedlings, also contained somewhat similar

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elongated particles. Some of these were cellulose fibres, but later work makes it probable that others were potato virus S, then unknown but soon to be discovered and, ironically, to prove to be related to paracrinkle virus.

Virus-free King Edward. The transmission of paracrinkle virus by sap inoculation and the knowledge about its morphology and properties brought it into line with other viruses and, by abolishing its seeming uniqueness, also abolished the need to assume any different relationship between it and the King Edward potato than between any other virus and a tolerant vegetatively propagated host. The idea that paracrinkle virus derives from a plasmagene or other endogenous component of King Edward was finally disproved by the demonstration that not every cell contains it and that, as with some other viruses, the stem apical meristems are not infected. Applying this knowledge and culturing apical meristems on nutrient medium produced a virus-free clone of King Edward (Kassanis, 1957), something heat therapy had failed to do (Bawden, Kassanis and Nixon, 1950). Most apical meristems did not differentiate and yielded only callus tissue, but one grew into a plantlet, which was virus-free. When large enough to handle, it was grafted on to a tomato plant, and after it was well established as a scion, cuttings were taken from it and established on their own roots. The resulting plants grew vigorously, producing enormous haulms, but when harvested in October none had any tubers, presumably because light and temperature conditions in the glasshouse were unsuitable for tuber formation. Further cuttings were taken, which were rooted and grown in controlled daylengths and temperatures, as were similar cuttings from the parent infected clone (Kassanis and Schwabe, 1961). Both clones then produced tubers, but comparisons of the plants showed that King Edward is not the perfect carrier of paracrinkle virus it had been assumed to be. Plants from the virus-free clone were more vigorous than the others, had more leaves and a larger leaf area, and produced more total dry weight and weight of tubers. Effects of the virus were also obvious when the two clones were grown side by side in the open, for plants from virus-free tubers were not only more uniform but their darker green, flatter and larger leaves covered the ground more completely than the foliage of plants from infected tubers.

The virus-free clone was multiplied under glass at Rothamsted from 1955 to 1957, when several hundred small tubers were given to the National Institute of Agricultural Botany to propagate in the field and conduct yield trials. The results of these trials, summarised in the table kindly provided by Mr. J. C. Cullen, show that the more vigorous haulm of the virus-free clone is reflected in an increased weight of tubers. The average of about 10% more yield than from the best obtainable commercial stocks comes from an increased number of tubers and not increase in size of tubers. A commercially desirable feature of the virus-free clone is that its tubers are more uniform in size, which is shown in the table by the fact that, although the weight of tubers passing over a 2-in. riddle is not much more than with the commercial stocks, the weight passing over a $1\frac{5}{8}$-in. riddle is.

The virus-free clone has now been extensively propagated and is likely

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soon to supplant other stocks, which means that, with no extra effort by growers, King Edward potato crops are likely to yield around 10% more in the future than in the past. The virus-free clone has produced variants with wholly red tubers, and so a virus-free line of Red King will also be able to take the place of the current infected ones.

Yields of tubers from the virus-free clone and seven commercial stocks of King Edward in trials by the National Institute of Agricultural Botany

Yield in Tons/acre

K = Paracrinkle Free Stocks A–G = 7 Commercial Stocks

	K	A	B	C	D	E	F	G
Total Yield:								
1959 (4 centres)	13·9	12·8	12·4	12·9	12·5	12·2	12·9	12·6
1960 (9 centres)	13·8	12·0	12·7	12·1	12·3	12·6	12·4	13·0
1961 (9 centres)	16·8	15·6	15·7	15·1	15·7	15·4	16·0	15·6
1962 (9 centres) *	16·7	15·2	15·6	15·5	15·6	15·6	15·7	15·2
1959–62	15·3	13·9	14·1	13·9	14·0	14·0	14·3	14·1
Yield Over 2 in.:								
1959 (4 centres)	5·0	5·5	5·6	5·7	5·4	5·3	5·4	5·6
1960 (9 centres)	7·4	7·4	7·5	7·1	7·1	7·5	7·1	8·1
1961 (7 centres)	12·3	11·9	12·1	11·6	11·6	11·4	12·0	11·4
1962 (9 centres) *	10·9	10·8	10·8	10·7	10·0	10·8	10·6	10·3
1959–62	8·9	8·9	9·0	8·8	8·5	8·8	8·8	8·9
Yield Over 1⅝ in.:								
1961 (8 centres)	14·9	13·7	14·2	13·4	13·9	13·7	14·4	14·0
1962 (9 centres) *	15·0	14·1	14·3	14·3	14·1	14·2	14·4	13·7
1961–62	15·0	13·9	14·3	13·9	14·0	14·0	14·4	13·9

* Stock C, D, E and F omitted at 1 centre.

Removing paracrinkle virus seems to have had no effect on the qualities of King Edward potatoes, except in vigour of its haulm and yield of tubers. Nor has it affected reaction to or susceptibility to infection by other viruses; in particular, the virus-free clone still retains its hypersensitivity to infection by virus X, and so it is unlikely that field crops will become infected with this virus.

Relationship with other viruses. Evidence relevant to the evolution of paracrinkle virus and suggesting that King Edward contracted it by infection with a virus carried by aphids came from an unexpected source, work on viruses infecting carnation (Kassanis, 1954, 1955). One of these, the aphid-transmitted latent virus, had particles indistinguishable from paracrinkle virus, and antiserum prepared against it precipitated specifically with sap from infected King Edward plants. This suggested a relationship between paracrinkle and an aphid-transmitted virus, but was not conclusive, because the antiserum also precipitated specifically with sap from seemingly healthy plants of other potato varieties, including Arran Victory. This fact became explicable when it was shown that these other varieties were infected by potato virus S, which was discovered by Ouboter (1951) while making serological tests during attempts to prepare an antiserum against potato virus A, and which she later found was prevalent in symptomless plants of many potato varieties grown in Holland. It has since been found to be widespread and shown to be serologically

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related to paracrinkle virus, which it accompanies in many King Edward plants (Kassanis, 1956, 1961; Rozendaal and van Slogteren, 1958; Bagnall, Wetter and Larson, 1959).

As all known stocks of Arran Victory were infected with virus S, the question arose as to whether the symptoms of plants infected from King Edward are caused by paracrinkle virus or by it acting jointly with virus S. To answer this, apical meristem culture was used to produce a clone of Arran Victory free from virus S (Kassanis, 1957), and this was infected with paracrinkle virus alone and together with virus S. The presence of virus S did not affect symptoms, and variability in their severity seems to depend solely on the virulence of the strain of paracrinkle virus. Indeed, the concept of the perfect carrier for long wrongly applied to King Edward and paracrinkle virus can perhaps be more appropriately applied to Arran Victory and virus S, for the virus-free clone is not noticeably more vigorous than its infected parent and has yielded little better in field trials. Also, it may be that King Edward is the perfect carrier of virus S rather than paracrinkle, for stocks infected with both viruses are not noticeably different from those infected with paracrinkle virus alone. However, the effect of infection on yield by virus S alone has not been tested.

Most pairs of serologically related viruses interfere with each other's multiplication, and plants fully infected with one resist invasion by the other, but this is not so with virus S and paracrinkle, each of which multiplies to much the same extent when together in plants as when alone. The lack of interference probably reflects the remoteness of the relationship between the two, shown by the fact that antiserum made against one may have a precipitation end-point exceeding $\frac{1}{1000}$ when titrated against that one, but fail when diluted beyond $\frac{1}{16}$ to precipitate the other. Kassanis (1961) suggested that viruses so slightly related serologically should be distinguished from one another by being called sero-types rather than strains, which should be restricted to those with closely similar antigenic behaviour. Accepting this suggestion, paracrinkle virus, potato virus S and carnation latent virus become sero-types of one virus, as also does chrysanthemum virus B, the latest to be shown to be remotely related to paracrinkle virus (Hakkaart, van Slogteren and Neeltje, 1962). However, in addition to virus S, paracrinkle is related to potato virus M, which causes leaf rolling mosaic and is so antigenically similar to paracrinkle that these two must be regarded as strains (Bagnall, Wetter and Larson, 1959). Leaf rolling mosaic is a common disease in North America, where it was described in detail before paracrinkle was discovered (Schultz and Folsom, 1923), so it takes precedence in nomenclature. Hence, paracrinkle not only ceases to be a name for an individual virus, but even of a distinctive sero-type, and remains only to identify a minor variant of the sero-type leaf rolling mosaic virus.

Transmission by *Myzus persicae*. The discovery that paracrinkle and the aphid-transmitted carnation latent virus are related raised doubts about the validity of the conclusion that paracrinkle virus is not transmitted by *M. persicae*, but first tests seemed to confirm the conclusion, for *M. persicae* failed to transmit the Rothamsted strain of paracrinkle virus in

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conditions in which it consistently transmitted the carnation virus (Kassanis, 1956). However, with the discovery that aphids also transmit the closely related leaf rolling mosaic virus (Rozendaal and van Slogteren, 1958; Wetter and Völk, 1960), further tests were made using King Edward plants from different commercial stocks as virus sources, and these showed that paracrinkle virus exists in strains that differ in their transmissibility by *M. persicae*, with some being transmitted readily and others only rarely, if ever. Thus, in conditions in which the Rothamsted strain was not transmitted to any of the test plants, three other strains were transmitted to more than half, to a third and to a tenth, respectively. (Kassanis, 1961)

After this knowledge it was not surprising to find that in some of the field trials conducted by the National Institute of Agricultural Botany, where plots of the virus-free clone were surrounded by plots of infected King Edward, a proportion of the initially virus-free plants became infected. The proportion differed greatly in different places and was most in districts where the aphid-transmitted leaf roll and Y viruses also spread most extensively. There have been very few infections in the crops grown in the recognised seed-growing areas, so the clone is unlikely to become reinfected, but it will clearly be necessary to test nuclear stocks regularly to ensure that they are still free from infection.

As no vector for potato virus S has yet been identified, it is of some interest that in the yield trials where the virus-free clone of King Edward became infected with paracrinkle virus it also became infected with virus S. Again there is the obvious possibility that virus S also exists in strains only some of which are aphid-transmitted and that glasshouse tests yet made have been only with strains not so transmitted. However, another possibility is that virus S is transmitted by aphids only when it occurs together in a plant also infected with an aphid-transmitted strain of paracrinkle virus, for several other viruses are known that are not aphid-transmitted when alone but become so in the presence of another virus that is. The early failures to transmit paracrinkle virus probably reflect the fact they were all made from a stock of King Edward infected with a strain not aphid-transmitted, which could also explain the lack of transmission when King Edward and Arran Victory plants were grown adjacent in the open, but an additional factor may be that Arran Victory plants, although they react so severely when infected, are much more resistant to infection by aphids than King Edward.

The surveys of commercial stocks of King Edward recently made show that most do contain aphid-transmitted strains of paracrinkle virus. There are various reasons for paracrinkle not being a prevalent disease in the United Kingdom despite the many sources of infection. First, varieties like Arran Victory that show severe symptoms when infected are rarely grown near to King Edward in districts where aphid-transmitted viruses spread readily, and it is even rarer for seed of such varieties to be saved in such districts. Secondly, aphids can become infective by feeding only briefly on King Edward, but they also soon lose their infectivity; this behaviour favours spread between plants within a crop rather than between separated crops, for few aphids will carry the virus over long distances. Thirdly, except for King Edward, the varieties commonly grown in the

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United Kingdom may be resistant to infection. The occurrence in North America of leaf rolling mosaic shows that in other conditions paracrinkle-like viruses can spread in field crops and cause damaging diseases. Aphids are more numerous there than in most parts of the United Kingdom, and there is some evidence that their virus strains are also more readily transmitted by aphids; also, their varieties may be more susceptible to infection. Whatever the explanation for spread in North America, the knowledge that paracrinkle and leaf rolling mosaic are related viruses emphasises the hazards to other varieties from growing infected stocks of King Edward, and provides an additional reason to the extra yield for replacing these stocks by the virus-free clone.

Surveying commercial stocks produced several other results. It showed that paracrinkle virus exists in strains of different virulence towards Arran Victory and that some King Edward plants contain strains causing a disease closely resembling leaf rolling mosaic; that most plants of King Edward are infected with potato virus S in addition to paracrinkle, and that not all plants have paracrinkle virus, for one was found infected with S alone. (Kassanis, 1961)

The origin of paracrinkle virus. From long being thought to be unique, the status of paracrinkle virus has steadily diminished, to become only one of many strains and sero-types in a group whose members differ in their host ranges, their virulence towards different species or varieties of plants, their transmissibility by aphids and, no doubt, in many other ways still to be discovered. What evolutionary significance to place on present knowledge can only be guessed at. Tracing evolutionary courses is difficult with organisms that leave fossil records, mutate rarely and have long generation times, and is impossible with viruses. However, it is plausible to assume that this group of viruses with now very dissimilar host ranges had a common origin in an aphid-transmitted virus that had a much wider host range than any of the existing members of the group yet studied. From what is known about the behaviour of other viruses, it is to be expected that, having entered plants as different as potato, carnation and chrysanthemum, the virus might change in different ways, for each host would preferentially favour any chance variant that multiplies more rapidly in it than the one that initiated the infection. Vegetatively propagated plants once infected remain so for as many generations as their progeny remains in being, and so provide ample time not only for mutants to be produced but also for them to be selected and become dominant. Not that any great length of time may be needed, for changing host plants is sometimes all that is needed to select forms differing by enough to justify distinguishing as sero-types, as when tobacco mosaic virus infects leguminous plants systemically (Bawden, 1958). Loss of transmissibility by aphids is not surprising, for the survival of a virus in a vegetatively propagated plant is independent of this property, which several other viruses have been found to lose when selection for it was not operating. The main thing that will be detrimental to the survival of a virus in clonal varieties of cultivated plants is virulence towards those varieties, for when selecting plants for propagation growers will reject those that are obviously diseased; no

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other explanation is needed for the fact that paracrinkle and the other viruses to which it is related are now prevalent mainly in varieties that are only little harmed by infection.

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