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An Analysis of some Necrotic Virus Diseases of the Potato.

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[Plates 3 and 4.]

Introduction.

The term " streak " has been applied somewhat indiscriminately to a variety of diseases of the potato in which the outstanding lesion is the appearance of necrotic patches in stem or leaf or both, such areas being more or less elongated. The first description of a disease of this type in the potato was made by Orton (1914) in 1912; a more detailed account of the same followed in 1920 (1920). Orton's description brings out certain salient points: in the diseases he describes the lesions are first seen in the adult leaves about one-third of the way down the stem as elongated spots which follow the veins and invade the parenchyma, and when viewed from the under surface of the leaf are seen to follow the veins as discoloured streaks. The disease spreads with great rapidity on the plant, the petioles become involved and collapse and, as a consequence, the leaf withers and hangs by a thread to the stem. The stem itself becomes brittle, turns brown, and dies at a point below the tip. The discolouration is superficial and apparently does not involve the vascular bundles. He observed no lesions in the tuber. Orton further noted the fact that whilst certain varieties such as Factor (Up-to-Date) were highly susceptible, many seedlings appeared to be immune. He could find no pathogene for this disease. Murphy (1921) described two conditions which he denoted as streak and leaf-drop; it would appear that the former is merely the seasonal, the latter the secondary form of one and the same affection.

Schultz and Folsom (1925) give a description of an affection in Green Mountain which corresponds closely to that given by Murphy for his streak. Atanasoff (1922, *a*) gave a full account of this same disease as exhibited in Duke of York and President. Most of his conclusions are based on the behaviour of the former variety, which is unfortunate, for, as we shall see, the Duke of York or Schottische Muis, as Atanasoff calls it, is a frequent carrier of another type of streak. Later, Atanasoff (1923—1925) mentions that this same streak could be transmitted by sap inoculation and by aphides, a characteristic of the streak

under discussion. He (1922, *b*) has laid all workers under an obligation by his research into the history of the so-called degeneration diseases of the potato in general, and particularly in his attempt to track down this particular disease as the evil genius of the potato from 1775 onwards. Recent work which has shown this disease to be due to a single aphis-carried virus, adds much strength to this claim.

Quanjer and Botjes (1929) describe no less than eight various types of streak, four of which are of the leaf-drop type, and three belong to a different group to which they have given the name top-necrosis. The first four groups are named, one after Atanasoff and the remaining three after the varieties in which they are said to be most characteristic. These four groups are probably merely variants of the same disease induced by a single virus in varieties some of which are themselves carriers of other viruses ; the fifth, sixth and seventh group are all examples of the streak referred to as top-necrosis, this time grouped according to the varieties in which they are latent. We owe these authors a debt of gratitude for bringing into relief the very real distinction between these two main types of streak and may ignore the unreal distinctions involved in their further sub-division, which have not only failed to obtain acceptance but have been completely superseded by later contributions of Quanjer (1931) himself. Here, recognising that the same virus will react quite differently on different varieties—a fact which had been already demonstrated by Salaman (1930, *b*)—Quanjer has introduced a classification of virus diseases based on the histological changes, more especially those which display the location and nature of the necrotic lesions. In this, Quanjer based himself on the valuable work of Artschwager (1923) who described streak lesions of the stem as proceeding acropetally in the vertical plane, and centripetally in the horizontal. In this last work Quanjer (1931) has built up a classification, on an anatomical basis, of potato virus diseases which exhibit necrotic lesions, which allows of the formation of six groups, three of which, viz., those dealing with phloem necrosis, phloem parenchyma necrosis of the tuber, and concentric necrosis of the tuber, we are not concerned with. A consideration of the remaining three groups in the light of new facts forms a considerable part of the subject matter of our communication.

Section 1 (Quanjer, 1931). *Anecrotic Mosaic.*—" No necrosis, no streak, no drop of the lower leaves of other varieties after they have been grafted with the virus-carrying scion ; only mottling and more or less wrinkling of leaflets." Here are included " mild mosaic, intermediate mosaic,* crinkle mosaic or

* The writers are not aware of the significance to be attached to this term.

interveinal mosaic." They are both sap and aphis transmissible. X-bodies are present, striate material absent. Quanjer states that should one of these be found on communication to another variety to induce necrosis, it must be removed from this group.

This provision of Quanjer's illustrates the unreality of a classification based on anything else than the nature of the ultimate constituent virus actually at work. Kenneth Smith's (1931, *b*) work has shown that these diseases are not all aphis transmissible, but that only one constituent of them is so, and Salaman (1930, *b*) has shown that whilst they may be communicable by graft they are not so necessarily by sap infection ; he (1932) has also shown that all these diseases will produce a streak on one or other variety.

Section III (Quanjer, 1931). *Top-necrosis—Acronecrosis.*—" Necrosis radiating from only a rather small percentage of the internal phloem strands, almost never from the external phloem strands, into the surrounding parenchyma, this in turn surrounded by a cork cambium, except in the tender tips which are soon killed ; occurring in foliage, stem and tuber."

Section IV. Acropetal Necrosis.—" Necrosis chiefly in the collenchyma of the leaf veins, petioles, and stems, in cases extending gradually to other tissues, no restriction by a cork cambium. The advance along the stem is acropetal ; dropping of lower leaves. Rugose mosaic and a part of the disease collectively known as crinkle and streak are characterised by this type of necrosis."

The data and conclusions here presented, support Quanjer's classification in respect of Groups III and IV, the former of which, however, must now be divided into at least four sub-sections.

The next advance in our knowledge, and by far the most vital, was the discovery and isolation by Kenneth Smith (1931, *a*, *b*) of the two unit viruses, X and Y. We shall be able to show that the major part, if not the whole of the acropetal necrotic group, is to be accounted for by simple infections with the Y virus, or, in certain cases, by the infection of this same virus superimposed on an existing virus complex carried by the plant in a latent condition. In this latter case the symptoms may be modified, as in Schulz's Green Mountain streak. Indeed, it is to the prevalence and unsuspected specificity of carriers that much of the confusion which has shrouded the subject must be ascribed.

We shall further be able to show that top-necrosis in some varieties is due to the action of the X virus alone, whilst in other varieties it is the sequela of a complex of which some of the constituents are known. The existence of a third virus element, Z, has been demonstrated by Salaman (1932), but the part

it plays in the composition of streak-producing complexes is in most cases still to be determined.

The survey of the literature to date allows us to distinguish two clearly differentiated clinical diseases under the headings of :—

A. Acropetal necrosis = stipple streak = leaf-drop streak.

B. Acronecrotic necrosis = Top-necrosis, Quanjer, and the streak of some older writers.

As long as we bear in mind that both these names are employed as terms to distinguish actual clinical pictures and do not necessarily correspond to the reactions of specific unit viruses, they are of value ; directly they are regarded as the inevitable reaction of a specific virus, or group of viruses, on the potato they are misleading and dangerous.

Our communication deals with these two clinical pictures—the behaviour of their causal virus or virus groups on different varieties and the demonstration that such groups may themselves be differentiated by these reactions.

A description of the histological character of the lesions will be found in a paper by F. C. Bawden (1932).

For comparison the two types of necrosis will be here described as exhibited on the variety President.

Acropetal necrosis as seen in the variety President. The following description is based on a large number of infections of President, both by inoculations and grafting with Kenneth Smith's Y virus ; the symptoms do not in any way differ from those induced by Smith by infections with the same virus by means of *Myzus persicæ*.

One stock of the Y virus in a Majestic seedling came direct from the cultures of Dr. Kenneth Smith, to whom we wish to express our grateful thanks. Another was from a plant of Epicure which was discovered by one of us in the field in 1930 and extensively studied. We had elucidated most of the reactions of this virus before we realised that the virus with which we were working was identical with the Y virus that Kenneth Smith had isolated earlier and described a little later.

The first symptom usually appears about 28 days after infection and consists of a blotchy mottle spreading from the veins and affecting the uppermost leaves only. This mottle later becomes intensified and is accompanied by some wrinkling and waving of the leaves, thus producing the picture of a crinkle. A little later necrosis appears on the underside of the veins of those leaves occupying an intermediate position on the stem, the upper surface of which may for a time look normal. These necroses increase in severity and spread

most rapidly along the course of the veins on the under surface of the leaf, appearing as elongated brown stripes on the petioles and as blotches between veins; later they penetrate the leaf tissue and become evident on the upper surface. The necroses pass down the petiole to the main stem and the leaf then collapses, rapidly withers, and remains hanging, as it were, by a thread, fig. 1, Plate 3.

Beneath the hanging leaves the stem frequently exhibits elongated brown stripes, but does not itself collapse as in the case of top-necrosis. This dropping of leaves following on the necrosis commences below and advances acropetally until in severe cases all the leaves except those at the very top may be seen hanging or have fallen to the ground. The topmost younger leaves rarely show any marked necroses, but they may become highly crinkled.

Infected plants die early and the tubers are of necessity few and small, but otherwise appear to be perfectly normal. Both necrosis and leaf-drop appear to be a first year or seasonal reaction, and though rather more striking and severe when the plants are grown under glass, are of the same general character when grown in the field. When the infection occurs naturally in the field as a result of aphis infection, symptoms do not make their appearance till well into July and the ensuing destruction is not so great as that which may be induced in the house. In their second year, under glasshouse conditions, after infection plants show but little sign of either necrosis or leaf-drop; they are small and stunted, their leaves and stems highly brittle; the internodes are short, and the leaves, generally mottled, are severely twisted and waved and bunched together, fig. 2, Plate 3. In the field, infected President plants in their second year present a picture which in extreme cases may resemble that of curly-dwarf.

Several infected plants have been examined for the presence of intracellular inclusions, or X-bodies, and none have been found.

Top-necrosis on President.—The first symptom which appears in about 15 to 20 days after grafting* consists of numerous minute irregular necrotic spots on the small folded leaves which make up the growing points, fig. 3, Plate 3. These necrotic lesions appear equally on veins and in the interveinal areas, rapidly increasing in size until by coalescing they destroy the small leaves and finally the whole top of the plant. The disease then spreads from above downwards, involving the stem as it goes. If the plant be young, it may be com-

* Not all top-necroses can be sap inoculated; indeed, if President be the test plant used, most cannot be so communicated. The acropetal necrosis can always be communicated by needle.

pletely killed out within a month. If, however, the plant is older, only the top and younger parts of the plant are killed outright. If the plant survives the first onslaught, further necroses may appear on the lower leaves as large blotches which penetrate the whole leaf tissue ; they do not spread rapidly and the leaf may fall and wither, but does not hang in the characteristic manner of the Y infected plants, fig. 4, Plate 3. The absence of all mottling is a feature in the acronecrotic type in President which further distinguishes the two types of streak. Plants infected when young rarely produce any tubers. If such are formed the majority exhibit definite and distinctive lesions during storage, although normal to all appearance when harvested. Such tubers are small and mis-shapen, fig. 5, Plate 4 ; they exhibit deep fissures or ulcerous depressions. The eyes are frequently destroyed by similar necroses and consequently they rarely sprout in the following spring, fig. 6, Plate 4. On section, such tubers exhibit large darkly coloured necrotic areas which extend centripetally and frequently result in the entire tuber being converted into a more or less spongy, corky mass. Tubers which are normal, *i.e.*, develop no necroses, will sprout and develop normal and healthy plants ; if a plant does grow from an infected tuber, it rarely develops, but when such does happen the resulting plant is dwarfed and extremely brittle, its leaves drop before they have unfolded, and the whole dies within a short time, fig. 7, Plate 4.

The descriptions here given for these two-streak types, as seen in President, agree closely with those given by Atanasoff and Quanjer ; indeed, in regard to top-necrosis, we are in full accord with the latter author's description of the disease in President. There is, however, a difference between our findings in regard to the tuber condition in acropetal necrosis. Atanasoff pictures deep ulcerous depressions in corky mis-shapen tubers of affected Duke of York in their second season, and blister-like swellings and superficial erosions in the same variety in its first season. Quanjer depicts very superficial necrosis in otherwise normal tubers following a seasonal infection. We find no such lesions, and the reason may lie in the fact that we have infected our virus-free material with a single virus, viz., Y, whilst Atanasoff, employing green-flies as vectors, unconsciously infected plants which were not virus-free but carried other viruses in addition to the pure Y virus, for it is this virus alone which the aphis transmits from a mixture. Quanjer, on the other hand, has used virus-free material as the subjects for infection, but his source of the virus is contaminated, viz., Zeeland Blue, and his method of infection, viz., core grafting, is particularly adapted to convey all the virus elements which may be present.

We may conclude that these two clinical types of virus disease differ in their mode of attack on both haulm and tuber.

We know of no causative agent for acropetal necrosis or leaf-drop streak other than the Y virus, but the reader is referred to Salaman's (1932) account of the reactions of that virus on varieties of the potato, from which it appears that leaf-drop streak is only developed in a few of our better known varieties, such as Arran Banner, Majestic, and Up-to-Date.

For further reactions on other Solanaceæ the reader is referred to Dr. Kenneth Smith's work (1931, *b.*).

The Acronecrotic or Top-necrosis Group of Streaks.

Just as we have seen that the Y virus will evoke a whole gamut of reactions according to the variety infected, so too does the X virus, but in this case the necrosis is typically acronecrotic. The reader is referred to the same source for a description of the reaction of the X virus on varieties of the potato. Out of 19 examined, 3 only respond with a top-necrosis, viz., Arran Crest, Epicure and King Edward; all the remainder display an interveinal mosaic.

For the reaction of this virus on other Solanaceæ, see Kenneth Smith (*loc. cit.*).

Top-necrosis—Section X.—Top-necrosis is seen in Arran Crest, Epicure, and King Edward. To take the last first: the X virus was inoculated into six plants, and all developed acute necrosis of the growing points in 15 days, which in most cases killed the plant. The tubers are either free of lesions or show the destructive necrosis and cork formation already described. In the second year the seed tubers either fail to sprout or produce healthy plants.

King Edward is a constant carrier of the Paracrinkle complex which contains the two virus entities Z and Y. Till we can obtain a King Edward free from this complex, we cannot say whether the top-necrosis developed is due to X itself or induced by a new complex which may possibly be formed by the interaction of the latent Paracrinkle and itself.

With Epicure and Arran Crest the case is, as far as we know, simple. We have stocks of either variety which we believe to be virus-free—or perhaps it would be more correct to describe them as stocks which have not yet been "found out." In these, an acute necrosis of all the growing points sets in in 14 days and kills the plants. This has been observed five times in Epicure and three times in Arran Crest. Second season plants of both varieties have proved to be quite healthy when raised from tubers which were free of visible lesions.

In this section infection can be equally well induced by inoculation as by

grafting. No insect vector has so far been discovered. Intracellular inclusions or X-bodies occur in all the X-infected plants that have been examined which exhibit mosaic symptoms. In one top-necrosis due to the X-virus in Epicure, none were found; presumably the advance of the disease was too rapid for their formation.

In the course of the experimental work of the last four years, the senior author has found, as have other workers, a number of varieties, many individuals of which are carriers of a virus or virus complex which, when introduced into Arran Victory or President, induces a top-necrosis streak. Salaman (1930, *b*) divides these carriers into two sub-groups, A and B, basing the distinction on their varietal reactions; our investigations fully support this sub-division.

Top-necrosis—Section A.—The varieties Arran Banner, Arran Consul, Green Mountain, Majestic and Up-to-Date, can carry without exhibiting any symptoms a virus complex which, when communicated by grafting to healthy President or to Arran Victory, occasions an acute top-necrosis in both varieties. A similar complex occasioning the same reaction is to be found in most samples of Duke of York and not a few of Eclipse. In these latter varieties, however, the virus is not strictly latent for they may themselves show evidence of disease, the Duke of York often developing a vague mottle and the Eclipse a more definite and blotchy one—in neither case are the plants noticeably disabled. The acronecrotic streak developed on the two test varieties is the same, whether the infection reach them from the true carrier varieties or from those which show some sign of disease themselves.

That the virus complex is the same in all is extremely probable, for we have found that reciprocal grafts between the carriers produce no reaction, which goes to prove that each of the six varieties is infected by the same virus complex, for each can carry its fellow's burden.

When Tobacco and Datura are inoculated with the juice from any one of these six varieties, the former reacts by a definite clearing of the finer veins of the young leaves, indicating the presence of the Y virus, whilst rings on the inoculated leaf, followed later by necrotic patches on the older ones, indicate the co-existence of the X virus. The Daturas react to all the sources with a severe mottle in which later green bands form alongside the veins, a reaction which is common to the X virus. On Tomato, inoculations produce a faint mottle, but if Tobacco mosaic be added to the inoculation, then a streak with leaf-drop ensues. This is the reaction which Valleau and Johnson (1931) claim to be pathognomonic for the so-called healthy potato virus, and which they find is always present in the variety Green Mountain. A stock of this

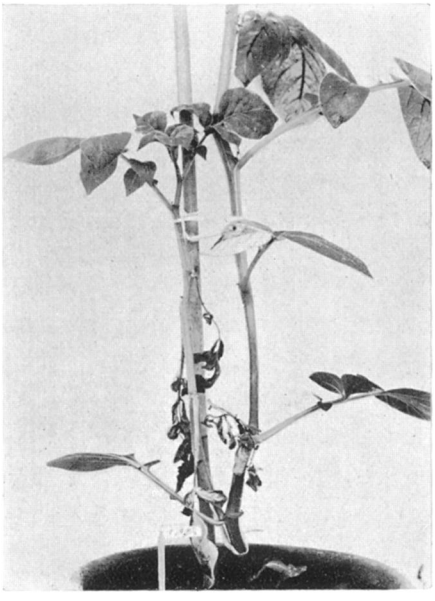

FIG. 1.

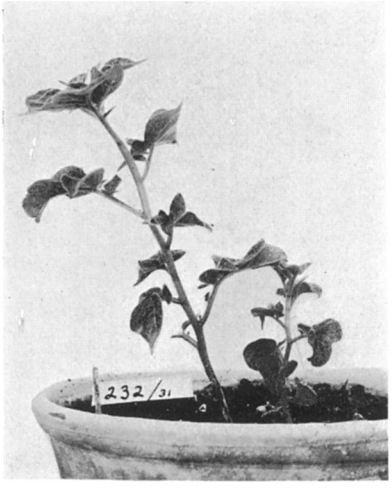

FIG. 2.

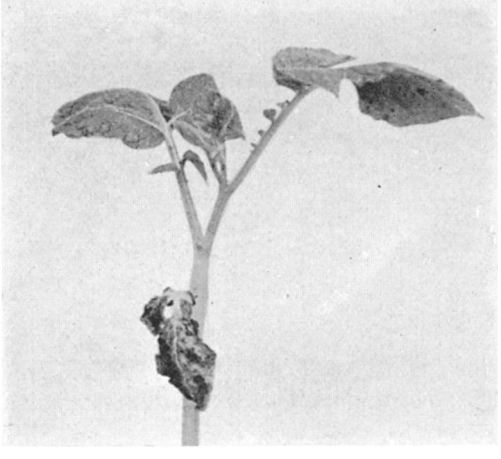

FIG. 3.

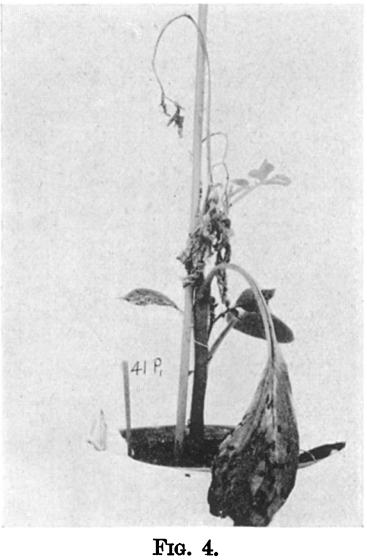

FIG. 4.

(*Facing p.* 60.)

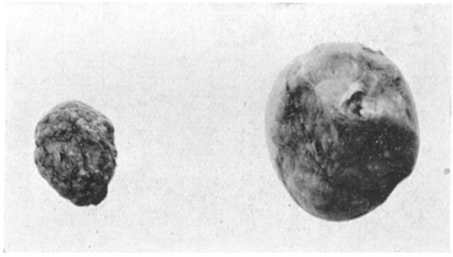

FIG. 5.

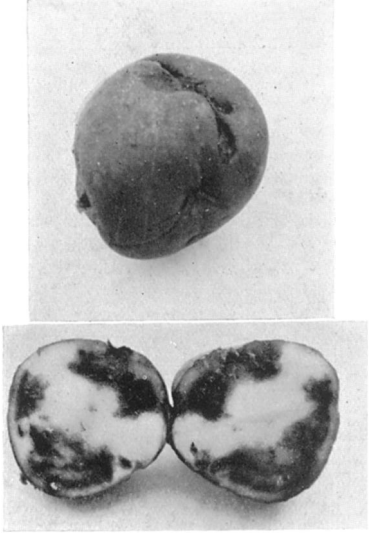

FIG. 6.

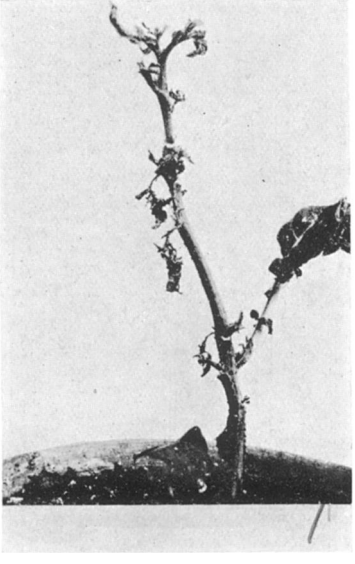

FIG. 7.

variety kindly given the senior author by Dr. Schultz as "healthy" in 1927, was found to be carrying this virus complex of top-necrosis.

Actually the presence of the Z virus has not been determined. Inasmuch as top-necrosis symptoms cannot be evoked by inoculation in any of the varieties examined (see Table I), except in Epicure and Arran Crest, we may assume that the complex responsible contains some element which renders it uninoculable. In the case of Paracrinkle, where the uninoculability is a constant feature, the presence of the uninoculable virus Z in the causative complex suggests that it is this virus which may be in some special manner responsible. It is therefore not improbable that the top-necrosis virus under consideration contains an uninoculable virus similar to the Z described, in addition to the X and Y we know are present. That the two varieties Arran Crest and Epicure react on inoculation is not surprising, for these varieties develop a top-necrosis, as we have already seen, on infection with a pure culture of the X virus. It is difficult to avoid the assumption that this sensitiveness of Arran Crest and Epicure is consequent on the ability possessed by their juices to break up the complex on contact and absorb forthwith the X. Other varieties after attempted inoculation give no evidence of the presence of any free X which we know would normally produce a mosaic in all of them; nor indeed evidence of the presence of any other recognisable virus. When sub-inoculations were made to Epicure from inoculated symptomless plants of Arran Victory, Arran Chief and President, there was no reaction in the former variety, which supports the view that the complex is not broken up, but rather that it is rejected as a whole by these varieties.

The juice of plants carrying top-necrosis A was inoculated into seedlings of certain wild potato species, viz., *S. utile*, *S. papa silvestre* and *S. antipovitchii*; all seedlings of the latter species reacted with the production of necrotic patches on the leaves, and vein-banding; it is probable that the cytoplasm of this unrelated stock disrupts the complex in much the same way as does that of Arran Crest and Epicure.

The virus complex common to the six carrier plants in which it has been found to exist in the field has been artificially communicated by grafting to a number of other varieties with the results as found in Table I.

In this table the division between those which are proved carriers and those which are probably such is purely temporary, the latter group not having been subjected to sub-culture to prove whether or not any virus is present. On the other hand, the two varieties, Duke of York and Eclipse, showing mosaic

Table I.*

—	Found in the field as carriers.	Infection by graft.	Infection by needle inoculation.
Top-necrosis with no mottling—			
Arran Chief		2/2	0/2
Arran Crest		1/2	2/2
Arran Victory		6/7	0/6
Epicure		1/1	2/3
Kerr's Pink		1/2	—
King Edward		2/2	—
President		5/6	0/5
Sharpe's Express		1/1	0/2
Mosaic—no streak—			
Duke of York	+	1/1	—
Eclipse	+	1/1	—
No symptoms but proved carriers—			
Arran Banner	+	0/1	—
Arran Consul	+	0/2	—
Di Vernon		0/1	—
Green Mountain	+	—	—
Great Scot		1/2	—
King George		0/1	—
Majestic	+	0/2	—
Up-to-Date	+	2/2	—
No symptoms—probably carriers—			
Arran Comrade		0/1	—
Champion		0/2	—
Rhoderick Dhu		0/2	—
No symptoms and no infection—			
Abundance		0/4	—
Tobacco—			
27 of the 55 reactions definitely demonstrated Y as well as X		—	55/57
Datura—			
X symptoms displayed		1/1	35/48

* The fraction against each variety represents as regards the numerator the total number of plants showing a reaction, and as regards the denominator the total number of plants used.

symptoms have been proved by us to contain the same complex as the true carriers and to communicate the full top-necrosis to susceptible varieties on grafting.

We have in Table I introduced under the group-heading " No symptoms— No infection " the variety Abundance, and we have done so with hesitation.

In the course of five years' intensive study of the virus diseases in the potato, we have failed to meet any unequivocal evidence for the presence of any true resistance to any virus disease in any variety. If we cannot communicate a virus entity or complex by the needle, we can always induce an infection of

some kind by means of grafting, and apparently it is the whole complex which passes to the host by this method. A virus may be, and often is, as we have seen, carried by a variety, but that is clearly a different phenomenon to that of resistance. Possibly it is expecting too much that there should be an absolute resistance to any virus, simple or complex, but we are bound to seek for any evidence which might show that a variety may reduce the virulence of a virus (or alternatively excite it) by passage through its tissues. We have no substantial evidence for such an action, apart from that to be now adduced in respect to the variety Abundance, which in itself is by no means conclusive. On the other hand, there are several considerations and some facts besides those about to be recorded, which induce a strong suspicion that in the course of vegetative propagation from year to year some virus elements may suffer such a loss of virulence within the tissues of a plant as to be finally unrecognisable, and that under certain circumstances some degree of virulence may be once more attained.

The virus-free stocks of Abundance, *i.e.*, those stocks which have never been found to produce a reaction on our test plants Arran Victory, President, Tobacco, or Datura, have been grafted on four occasions with the top-necrosis virus, twice from Up-to-Date and once from Majestic, and once from Arran Consul carriers. In three cases there was no response whatever, although the grafts were good and grew freely. In the fourth case there was a slight clearing of the veins after 3 weeks, from which the plant entirely recovered, but at the tenth week after grafting, when both scion and stock were maturing, a few veinal necroses appeared. Scions were removed from this same plant 7 weeks after the grafting and put on healthy Arran Victory and President; in neither case did the stock plants exhibit any reaction.

The evidence is suggestive of the existence in the variety Abundance of a definite resistance to certain viruses. Salaman (1930, *b*) pointed out that this variety behaved in a peculiar manner to Crinkle A. We now know, Salaman (1932), that the virus content of the infecting crinkle was Z + X: on Abundance it produced but the mildest mosaic, and when returned to President it gave an interveinal mosaic and not a crinkle, which suggests that the action of the Z virus had been eliminated somehow. Datura inoculated from the infected Abundance gave a similar reaction to that evoked by the virus X, which shows that it had at any rate accepted this virus. In the same communication an account is given of the reactions of an Abundance in the field in which the leaves were a trifle rugose but in which there was no mottling; here, two consecutive passages through President reduced the reaction to vanishing point,

whilst in a similar passage through Arran Victory the plants were found to react with a mild but definite picture of Crinkle A. Here the evidence again points to an action of the Abundance on the Z virus which we may regard as attenuated in the juices of Abundance and which does not regain its vigour in the juices of President, but does do so to some extent in Arran Victory. An attempt was made to discover whether Abundance juice had any direct action on the X virus; leaves of healthy Abundance and of President plants bearing the X virus were ground up and incubated at 70° F. for 1 hour and then inoculated into plants of the following varieties—Abundance, Arran Crest, Arran Victory and President. The Arran Crest reacted promptly with a top-necrosis, as it always does to the X virus; King Edward failed to react; but President and Arran Victory developed interveinal mosaic of the same intensity as did the controls to the X virus alone. The evidence, though negative, goes to support the contention that the element which Abundance influences is not the X but the Z virus. An experiment in which a scion of X-bearing President was passed through an intermediate scion of Abundance, itself grafted to a healthy President, yielded a similar result, *i.e.*, the basal President stock responded with the normal interveinal mosaic reaction.

Top-necrosis—Section B.—Salaman (1930, *a*) drew a distinction between two groups of top-necrosis based on their reactions on the standard test varieties Arran Victory and President. Whereas in the A group both of these varieties go down with an acronecrotic streak, in this group President suffers an acute top-necrosis, Arran Victory only a rather mild veinal mosaic.

We have discovered but one variety in which this particular virus complex is latent, and that in only a few of its stocks. The variety is Di Vernon, and it was found in certain tubers collected in June, 1928, from healthy and vigorous plants in the field.

The varietal reactions of this latent virus as obtained by grafting are as follows:—No reaction of any kind was obtained by inoculating the juice of the Di Vernon source in the varieties specified in column 2 of Table II.

The group which displayed "No symptoms" in Table II must not be assumed to be carriers, for sub-grafts were made from Arran Crest, Sharpe's Express and Great Scot to President without effect. The difficulty of making successful grafts with Di Vernon adds an element of uncertainty to any negative results. On the other hand, all Arran Victory plants which displayed a mosaic as a consequence of infection with this virus reacted on grafting to President by inducing a lethal top-necrosis.

The absence of a reaction following inoculation on any of these potato

Table II.*

—	Infection by graft.	Infection by needle inoculation.
No symptoms but carried by—		
Di Vernon	1/1	—
Top-necrosis developed—		
Arran Banner	1/1	—
Arran Consul	1/1	—
Duke of York	1/1	—
Eclipse	1/1	—
Epicure	2/3	0/2
King Edward	1/3	—
Majestic	1/1	—
President	4/5	0/4
Up-to-Date	2/3	—
Mosaic—		
Abundance	2/2	—
Arran Chief (very mild)	1/1	0/2
Arran Victory	4/5	0/4
Kerr's Pink (very mild)	1/1	—
No symptoms—		
Arran Crest	2/2	0/2
British Queen	1/1	—
Great Scot	1/1	—
International Kidney	2/2	—
Sharpe's Express	1/1	—

* The fraction against each variety represents as regards the numerator the total number of plants showing a reaction, and as regards the denominator the total number of plants used.

varieties should be reviewed in the light of the reaction of this Di Vernon complex on Tobacco and Daturas.

On Tobacco we find a pure and definite Y and no sign of an X reaction. But this Y reaction is not obtained readily; in the first batch of nine tobaccos, only one reacted with clearing of the veins, an early symptom of Y infection, and then recovered. In a second batch of six plants inoculated later in the season, three reacted quite definitely with well-marked clearing of the veins and later a striking vein-banding. It is clear that this virus complex does not readily break up even in the foreign environment of a different species, such as Tobacco.

Top-necrosis A was inoculable only in the varieties Arran Crest and Epicure, both of which are highly susceptible to the X virus. Apparently a complex is rather more stable when X is absent than when it is present. In this respect one is reminded of paracrinkle, which is likewise free of any X virus and which can be conveyed neither to potato, Tobacco nor Datura by inoculation. On Datura we failed to obtain a reaction of any kind on the 35 plants inoculated, which is further evidence against the presence of the X virus. On the other

hand, if this particular stock of Di Vernon be grafted to Datura, we get a peculiar reaction which is identical with that described by Salaman and Le Pelley (1930) as characteristic of paracrinkle. These same Daturas showed no evidence of the X mottle. In view of the fact that the scions grew well, there can be no doubt that whatever virus was present entered the Datura, hence we may conclude that no X was present in this particular complex. Salaman (1932) has recorded how paracrinkle might be synthesised by the addition of a Y virus to the virus complex latent in this Di Vernon. Paracrinkle we know contains the Z virus, hence this Di Vernon must presumably contain it also and, as we have shown by the tobacco reaction, it certainly contains the Y virus in addition.

The Di Vernon complex under review therefore may be regarded as built up of Z and Y.

The two complexes which we have described, both of them latent in different varieties, are thus seen to differ very considerably in their reactions, and we are able to show that one, top-necrosis B, is built up of the virus elements Z and Y; the other, top-necrosis A, is built up of X and Y and that possibly another uninoculable virus such as Z is present also.

We do not wish to infer that our analysis is in any sense to be regarded as final; there may well be other virus entities involved which remain to be identified.

Attempts were made to infect a plant simultaneously with top-necrosis B and the pure X virus, *i.e.*, with the elements Z, Y and X, and thereby possibly counterfeit the complex common to the A variety of top-necrosis. When this is done on President the result is a top-necrosis, but as this may equally be due to the Z Y, of the B top-necrosis as to any newly synthesised virus complex, it is not of any immediate value in the solution of the problem. On the other hand, if we add the X virus and the B top-necrosis complex to Arran Victory, then if the X is producing any effect either on its own or by entering into closer relation with the B complex, we might expect to get a result which would be unlike the mosaic produced by the B complex and might be similar to that induced by the A top-necrosis which we know contains X and Y possibly associated with a Z-like element. This particular experiment was done twice; the B top-necrosis was introduced by a graft, the X by inoculation. In one case a crinkle was produced of a much more severe kind than that called forth by the B top-necrosis alone. In the second, the scion conveying the B complex was poor, but a severe interveinal mosaic supervened in which some definite necroses occurred such as are to be found usually in Arran Victory

infected by the A top-necroses complex. From these preliminary experiments it looks as if it might be possible to convert the B top-necrosis complex into the A complex in Arran Victory by the introduction of the X virus.

A third top-necrosis complex has been discovered in a Great Scot " wilding " potato which was kindly given the senior author by Mr. Anderson of the Board of Agriculture for Scotland in 1927, as a good example of a " wilding." In 1928 it was grafted on to Arran Victory and President without producing a reaction. In 1931 the same stock was tested out again, when it was found to present certain distinctive reactions. We suggest that this type of streak should be referred to as the C top-necrosis.

Unlike the A or B type, we have not found it in a latent condition. The Great Scot " wilding " from which the virus complex was obtained has throughout the 5 years it has been under observation appeared a sickly plant, many-stemmed, with the leaves much broadened and poorly developed, exhibiting a mild veinal mosaic on a dark-green background with a rugose surface, with edges deflected.

The outstanding characteristic of this C type is that when grafted to Arran Victory it causes a very severe or deadly top-necrosis streak with the extremely short incubation period of 9 days; on President it produces a crinkle and no necrosis—in short it reverses the reaction of the B top-necrosis. In the following table the varietal reactions of the C type of top-necrosis, so far as we have discovered them, are given.

Table III.

Symptoms.	Infection by graft.	Number of plants tested and number reacting.	Infection by inoculation.	Number of plants tested and number reacting.
Top-necrosis with no mosaic or crinkle.	Arran Victory	2/2	—	—
	King Edward	1/1	—	—
	Sharpe's Express	1/1	—	—
Top-necrosis with crinkle or mosaic.	Abundance	1/1	Arran Crest	2/2
	Arran Crest	1/1	Epicure	2/2
Crinkle or severe mosaic with some necrosis.	—	—	Sharpe's Express	2/2
Crinkle or severe mosaic alone.	Duke of York	1/1	Arran Victory	2/2
	Great Scot.....	2/2	Great Scot.....	1/2
	President	2/2	President	2/2
			Up-to-Date	1/1
Severe mosaic with necrotic lesions.	Majestic	2/0	Majestic	2/2
No symptoms developed	Arran Chief	0/1	—	—
	Epicure ..... (scion poor)	0/1	—	—
	Up-to-Date ..... (scion poor)	0/1	—	—

On Tobacco the C type when communicated by needle has a peculiar reaction: at first there is a very definite local reaction of necrotic rings followed by a marked clearing of veins on which there supervenes a severe yellow necrotic etching of the veins. The leaves tend to fall and younger leaves succeed, again reproducing the clearing of veins and a fine spotty mottle. The reaction was observed in all of the nine plants inoculated. The Y reaction was most pronounced, much more so than the corresponding Y reaction of top-necrosis A. Later some of the younger leaves assume a peculiar appearance in that the lamina bulges upwards between section of the larger veins which do not seem to have kept pace with the remainder of the growing leaf.

A survey of the varietal reactions recorded in Table III shows that they are in many respects peculiar. The variety President, itself so susceptible to the top-necrosis complexes A and B, is but little affected. We have seen that, with the exception of the A type on Arran Crest and Epicure, both the A and B complexes are uninoculable. The C complex, on the contrary, is readily inoculable, though the symptoms induced thereby are not always the same as those consequent on grafting. Of particular interest is the reaction of the C top-necrosis complex on Majestic; on four different plants we found a severe mosaic on the upper parts of the plant, accompanied by necrotic lesions which conformed to the top-necrosis type; later veinal necroses with leaf-drop in the lower parts of the plant developed, which gave rise to a picture suggestive of an acropetal infection. It was as if two distinct diseases were acting more or less independently on the same plant.

We may point out that however distinct the exciting causes may be, the four different top-necroses in respect to their necrotic lesions differ neither in their general character, their distribution on the plant, nor histopathologically the one from the other. On the other hand, this particular complex produces in certain varieties a top-necrosis which differs from that produced by the other three, not in respect to the necrosis itself, but in the fact that the same plant exhibits mosaic symptoms which may vary from a mild mosaic to a crinkle.

Discussion.

The history of acropetal necrosis as a virus plant disease with the narrowing down of its symptoms to a series of varietal reactions, is a tale full of promise for its suggests that all the recognised virus diseases may ultimately be related to a specific virus or virus complex to which a specific range of reactions will be ascribed. Hitherto our views on virus diseases of plants have either passed, or are still in process of passing, through the phase when protean reactions

are mistaken for specific diseases and given special names. With the birth, or rather recognition, of the Y virus and its cogeners, the X and Z viruses, we may be permitted to look forward to the time when the idea that names such as mosaic, mild mosaic, rugose mosaic, crinkle, streak, and the like, connote separate disease entities, instead of mere symptoms often common to the action of a number of distinct infective agents, will be consigned to the limbo of outworn hypotheses.

In this particular instance we may be permitted to claim that a disease which has passed under very many different names, of which the more commonly known are leaf-drop streak or acropetal necrosis, is induced by one single virus, and that virus is Kenneth Smith's Y. It is further established that Quanjer's top-necrosis or acronecrosis is, both in its histological expression and in its causative agents, entirely distinct from the acropetal type. Of these causative agents it is established that in a limited number of varieties this disease may be induced by Kenneth Smith's X virus acting alone. We have learnt, however, that there are three other causative agents which will produce in one variety or another a top-necrosis ; and we have distinguished them by their varietal reactions and designated them as top-necrosis A, B, and C.

We have proved that top-necrosis A contains both X and Y and we suspect the presence of Z ; and that top-necrosis B contains Y and not X and that it almost certainly contains Z. We have further shown that top-necrosis C contains X and Y, but we have no particular reason to suggest that Z is present. Although the two complexes A and C do thus appear to show a like composition as far as our yet imperfect methods of analysis allow us to investigate it, we yet know that they are entirely distinct.

It has been suggested by Salaman (1932) that a virus complex is not a mere mixture but a more or less specific grouping of virus entities united in such a manner that the resultant group acts as a whole and excites reactions because of the characters which have come to it by reason of the specific grouping of its constituent units. Nothing could demonstrate this more forcibly than the fact that Up-to-Date plants carrying the top-necrosis A complex which undoubtedly contain the X and Y viruses, will succumb with a typical acropetal streak when they are further infected with the pure Y virus, a fact which would be difficult to understand were such complex to be a mere mixture. The reactions of the four acronecrotic groups would lend further support to this view of virus complexes.

Similarly, top-necrosis B contains the Z and Y virus, but so does para-crinkle, which has quite different reactions.

The problems which these facts present cannot be solved satisfactorily till we have more analytic work on virus entities; but a solution of the problem might be expected to follow on either of the three following lines: (*a*) that similarity of composition, so far as the mere presence of the three viruses X, Y, and Z are concerned, does not necessarily imply a similarity in the resultant complex as shown by its reactions; (*b*) that these diseases contain the same virus elements, but in different proportions; (*c*) that they differ by reason of a change of virulence in one or other constituent virus.

There does seem to be an especial importance in the relation between a complex and its environment, *i.e.*, the cytoplasmic characters of the host. The fact that top-necrosis complex A will react on inoculation on Arran Crest and Epicure only of the varieties tested and on seedlings of *S. antepovitchii*, a wild tuber-bearing Solanum, and not at all on those of *S. utile* and only occasionally on *Papa Silvestre*, emphasises this fact. It seems reasonable to suppose that in order to exert an action, an otherwise uninoculable complex must suffer disintegration on contact with the strange cytoplasm before one or more of its constituents can act. In Tobacco this process can in a sense be observed, a complex such as top-necrosis A will exert first a local reaction due to the X virus, then a clearing of the veins due to the Y, and at this point Kenneth Smith has shown that the Y virus can be recovered without its fellow, whilst the X, free from any Y, can be recovered from the inoculated leaf. In the potato such a separation occurs but rarely.

It is not proposed to discuss the problem here in further detail. The important question of inoculability versus uninoculability, the means by which X and Z reach the potato plant at all, the possibility of viruses losing their virulence after a long residence within the same plant, and the like, must all be considered before a satisfactory solution of the nature of the potato virus complexes can be envisaged.

The study of the virus complexes concerned in the top-necroses which, as we have seen, are so readily and frequently carried by varieties such as Majestic and Up-to-Date, which are grown on a very large scale, leads to a consideration of practical and economical importance. These carriers contain the virus Y; it is this virus which is so readily taken up and transferred by the ubiquitous aphis *Myzus persicæ*. The field crops of such carriers may give the farmer every satisfaction. Looked at from the pathologist's point of view, however, they are vast reservoirs of the most destructive of all the virus entities we know, dangers to other varieties, and even a danger to themselves, for a carrier Up-to-Date can go down to a further infection of the very virus Y which it itself is carrying.

We are indeed faced by a dilemma: either we must aim at growing only virus-free stocks—a possible though difficult and costly task—or we must use only such varieties as are successful carriers of the more serious virus diseases.

Summary.

A summary of the literature on streak is given, from which it appears that two distinct clinical states can be isolated.

One of these is that described by Orton and commonly known as stipple-streak or leaf-drop streak and later designated, on the grounds of its histo-pathology, as acropetal necrosis. The other, known as top-necrosis, has been described by Quanjer on the basis of its histopathology as acronecrosis.

It has been shown in that the former is the distinctive reaction in certain varieties of the Y virus of Kenneth Smith.

Acronecrotic or top-necroses have been shown to be divisible into at least four distinct groups based on their varietal reaction, and here designated as top-necrosis X, top-necrosis A, top-necrosis B, and top-necrosis C.

The first three are alike in that when they do produce a top-necrosis in any given variety, it is unaccompanied by any mosaic symptom. Top-necrosis C, on the other hand, differs clinically by the fact that necrotic and mosaic symptoms occur together.

It is shown that top-necrosis X is due to the action of the X virus acting alone.

Top-necrosis A is shown to be due to a complex containing both X and Y, possibly associated with the virus Z.

Top-necrosis B is shown to be due to a complex containing both Z and Y.

Top-necrosis C is likewise shown to be due to the presence of both viruses X and Y.

The top-necroses X and C complexes are capable of transmission by needle inoculation to other potato varieties, though it by no means follows that the resultant lesion is a top-necrosis. Top-necrosis B is uninoculable, and so is top-necrosis A, except that it can be conveyed to the varieties Arran Crest and Epicure by the needle.

Carriers of top-necrosis A are found amongst many of our widest grown varieties, such as Arran Banner, Majestic, and Up-to-Date; indeed the latter is rarely to be found without such latent infection.

A carrier of top-necrosis B has only been found in the field in the variety Di Vernon.

A clinical disease, it is held, cannot be defined by the syndrome of its reaction in one particular variety of the potato, but it is to be identified rather by the complete tale of its reactions in a large number of varieties, as well as in a certain number of selected species of the non-related Solanaceæ.

The view is put forward that our goal in the study of plant virus diseases and their classification should be to find a correct formula in terms of the virus entities concerned for each clinical disease.

A discussion of the results and their bearing on the theory of virus complexes is added, certain suggestions are put forward for consideration.

The bearing of these results on the raising of crops on an economic basis is considered.

EXPLANATION OF PLATES.

Plate 3.

Fig. 1.—Later stages of Y infection on President: necroses are spreading along large sections of the veins and are especially noticeable on the under surface of the leaf. The intermediate and lower leaves have died and dropped, consequent on the destructive action of the virus on the supporting tissue in the petiole. The apical growth is but mildly crinkled, and free from visible necroses.

Fig. 2.—A plant of President infected in the previous season with the Y virus. The photograph represents 3 months' growth. The plant is stunted, leaves poorly developed, twisted, and the surface mildly crinkled. There are no necroses and no leaf-drop, though both were present in the previous season.

Fig. 3.—The earliest stage of a top-necrosis as seen in President; the necrotic flecks are scattered indiscriminately on veinal and interveinal areas and are unaccompanied by mottling or deformity.

Fig. 4.—A President plant with advanced symptoms of top-necrosis. The upper part of the plant is already dead, the lower dying with large irregular necrotic flecks. The infecting virus complex is top-necrosis B.

Plate 4.

Fig. 5.—Small shrunken tubers of an infected Arran Victory plant: the tuber to left is completely converted into a corky mass; that to the right is partly so. On its outer surface deep fissures have appeared, the eyes are sunken and destroyed. The infecting virus complex is that of top-necrosis A.

Fig. 6.—A tuber from an infected President plant which has developed during storage ulcerous fissures; on section the cork is seen to be mainly on the inner side of the vascular bundles, but extends to the periphery in the neighbourhood of the eyes, which are destroyed. The infecting virus complex is the same as in fig. 7.

Fig. 7.—An Arran Victory plant in its second season after infection with top-necrosis derived from Up-to-Date. (Reproduced by kind permission of Dr. Kenneth Smith.)

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