INHERITANCE STUDIES ON 24-CHROMOSOME TUBER BEARING SOLANUM SPECIES.

Thesis

Submitted by

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INTRODUCTION

The work to be described in this paper has been carried out at the Scottish Plant-breeding Station as a part of the programme of research on resistance to potato virus diseases. The general background of this work has been reported in the Annual Reports of the Scottish Plant-breeding Station for the years 1930-1948 and details of particular investigations are to be found in papers by Cockerham (1937a,b, 1939, 1943a,b and 1945) and Cadman (1942).

Most of the work already recorded has been concerned with resistance qualities found in cultivated varieties of potatoes and in particular with the resistance, which has its foundation in the extreme intolerance or hypersensitiveness of the plant tissue to the invading pathogen, the intolerance being shown either in death of the whole plant, or in the death of the local tissue at the site of the virus entry. Both of these results of infection are considered to be different manifestations of the same basic plant response as plants which give either reaction on sap inoculation give fully systemic necrotic reactions when infected by grafting.

The reactions of hypersensitive cultivated varieties of the potato to viruses "X", "A", "B" and "C" have been fully described by Cockerham (1939, 1943a,b, and 1945) and Cadman (1942)under the terms, "top-necrosis", "apical top- necrosis" and "local lesion necrosis."

The terms "top-necrosis" was first applied by Quanjer and Botjes (1929) and Quanjer (1931) to a specific type of virus disease symptoms, characterised by the necrosis of the inner phloem strand followed by the death of the growing point and eventually by the death of the whole plant from top downwards. Quanjer's work was later confirmed by Bawden (1932).

In suitable material the disease is readily induced by infection through a graft union but much less readily by other forms of infection, such as, by sap-inoculation or, where applicable, by the feeding of infective aphids. More usually these latter forms of infection induce the formation of local lesions at the site of virus entry. As further symptoms rarely develop and as no virus can be recovered from the unaffected tissues of plants showing lesions only, it is concluded that the virus is restricted within the lesions.

The ability to respond in hypersensitive fashion is a character of considerable economic importance in the control of virus disease. Systemic necrotic symptoms are only rarely to be seen in the field and it seems clear that the localisation of viruses at their point of entry provides a mechanism through which intolerant plants may resist under natural conditions of infection.

There are many instances in which localisation of the pathogen through hypersensitive reactions gives rise to resistance to various fungal diseases. The reaction of the Norwegian "Viking" red currant to Cronartium ribicola, the white Pine blister rust, indicated that it owed its apparent immunity from attack by this fungus to the localisation of the pathogen in the small watery pustules which developed into necrotic flecks (Hahn 1929, 1936). Similar reactions were obtained in apple varieties resistant to infection by Gymnosporangium juniperi viginianae (Neũsbaũm 1935) and in one strain of onion, immune to Urocytis ceputae S/ (Evans 1933). The resistance of certain wheat varieties to Puccina graminis tritici, was described by Stakman (1915) as being due to the localisation of the pathogen through hypersensitiveness of the plants. The works of Johnson (1925) with tobacco mosaic virus in Nicotina glutinosa, of Künkel (1928) with grass a/ mosaic in sugar cane and Valleau and Johnson (1930) with tobacco mosaic in potatoes can also be quoted as instances of recovery and apparent immunity of the plants from the virus infection, associated with necrotic lesions.

In the case of potato viruses "X", "A", "B" and "C", it has been established that potato varieties which responded to graft infection with any form of top-necrosis are virtually free from losses due to the disease. Hence it has been concluded that the normal response of such varieties to infection in the field is that of localisation of the virus at the point of entry. Occasionally plants with full systemic necrosis have been found. In this case their death, including the death of any tubers reached by the virus, ensures no perpetuation of infected plants in the following year. Such varieties have been described, therefore, as field-immune.

Cockerham (I937) and Cadman (I942) showed that in cultivated varieties the hypersensitive reactions to viruses "X", "A", "B" and "C" are controlled by single dominant genes, N_x, N_A, N_B, and N_C respectively and Cockerham (I943 a, b,) has given an account of the availability of the genes in cultivated varieties of the potato. ? Hence during the last few years the hypersensitive character has been extensively used in potato breeding in seeking resistance to virus diseases.

More recently an examination of the wild potato species from South America has revealed similar hypersensitive characters in respect of not only viruses "X", "A", "B" and "C" but also of virus "Y": the latter having been reported in the "diploid" species, Solanum simplicifolium, in two clones of the "hexaploid" species, Solanum demissium, and in two clones of the "pentaploid" species, Solanum Salamanii (Cockerham I943, I946 and I947).

The present work consists of a study of the genetic background of hypersensitive responses to viruses "X", "A", "Y" and "C" in certain "diploid" (2n=24) species of the potato. It is concerned chiefly with the inheritance of hypersensitiveness to each virus and with the interrelationships of the various genes which appear to control this form of response.

Although 24 chromosome potatoes are usually regarded as "diploids" and I2 as the basic number of chromosomes in potatoes, cytological evidence has led a number of workers (Lawrence I93I~~a~~; Müntzing I933, Ellison I936~~a~~ and Choudhuri I943, I944) to suggest that the basic number is 6 and that the 24-chromosome potatoes are therefore "tetraploids". Genetic data on this material is scanty and gives no support to either point of view. Hence in the present investigation attempts have been made to throw some light on the general form of inheritance in the 24-chromosome potatoes with a view to examining the question of the polyploid nature of 24-chromosome species from the genetic aspect.

As already mentioned, the major part of the work is concerned with the inheritance of hypersensitive reactions to viruses "X", "A", "Y" and "C", but for the purpose of wider investigations the data obtained from the virus studies have been supplemented from a subsidiary study of the segregation of colour factors in identical and related material.

SECTION. 1.

INHERITANCE OF HYPERSENSITIVE REACTION.

Materials and Methods.

The materials used in this investigation consists mainly of progenies derived from the crosses, Solanum simplicifolium (C.P.C 5IA) x Solanum Rybinii (C.P.C I3II), Solanum brevimucronatum (C.P.C7I)x Solanum simplicifolium and their reciprocal crosses. Solanum simplicifolium is hypersensitive to viruses "A", "Y" and "C" and Solanum brevimucronatum to virus "X" only. Solanum Rybinii is susceptible, ie, non-hypersensitive, to all the four viruses Hence Solanum Rybinii and non-hypersensitive seedlings in some of the progenies were used as recessive parent in breeding, as it also proved to be non-hypersensitive to all the four viruses.

? the speci
or the seedl

Two other species, Solanum saltense (C.P.C.5IB) which is hypersensitive to virus "A" and Solanum jujuyense (C.P.C.84), which is hypersensitive to virus "X" were included in the original scheme of breeding mainly to raise material for the estimation of linkage between the genes controlling hypersensitive reactions to viruses "X" and "A". But as seedlings in the F_1 progenies from crosses between these species flowered sparsely or not at all, further breeding was not possible and the data obtained refer.only to the segregation of hypersensitiveness to viruses "X" and "A" as independent characters.

Figs. I, 2, 3, 4 and 5 show the family trees of the various progenies tested.

Fig. 1.

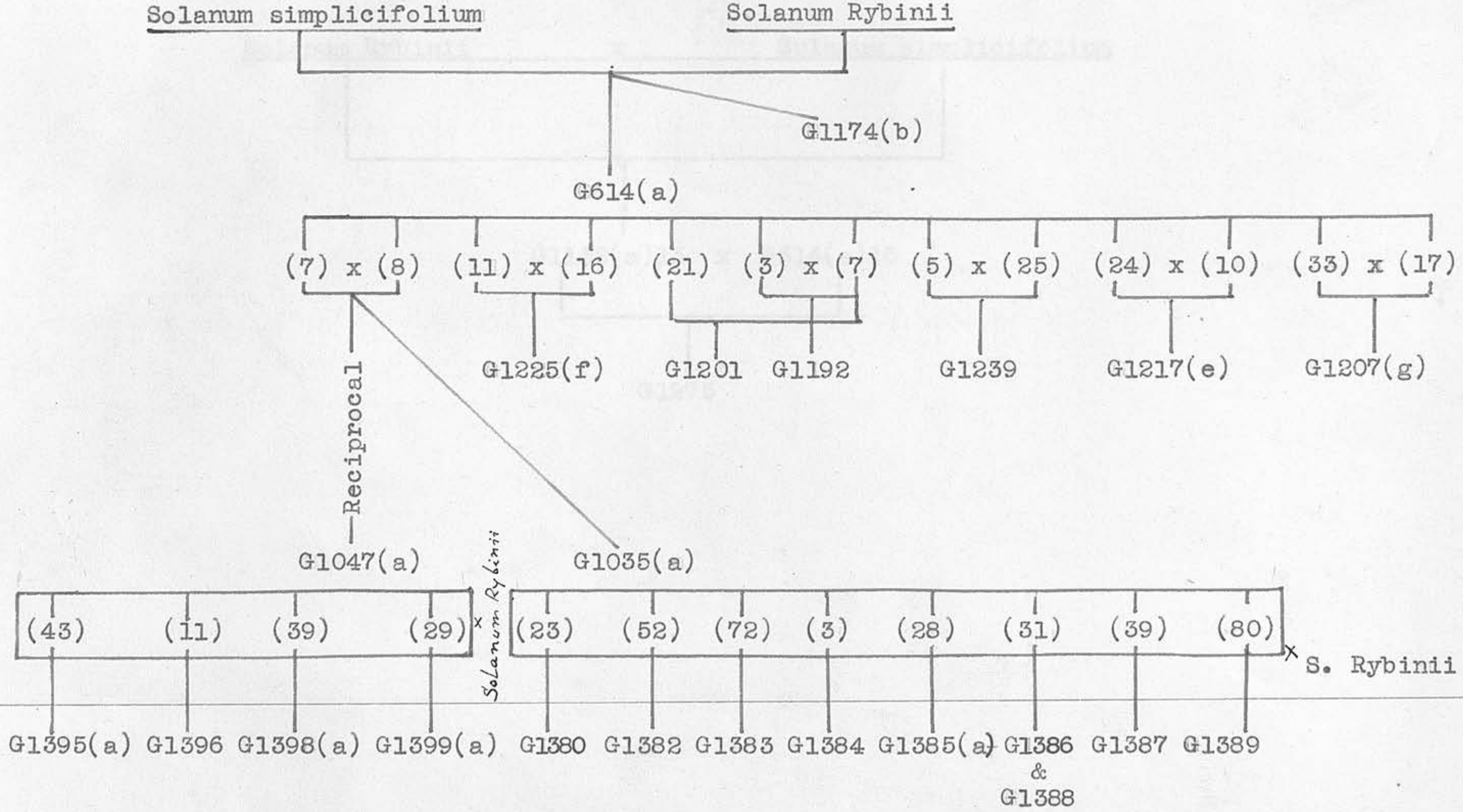

Solanum simplicifolium
Solanum Rybinii
G1174(b)
G614(a)
(7) x (8)
(11) x (16)
(21)
(3) x (7)
(5) x (25)
(24) x (10)
(33) x (17)
G1225(f)
G1201
G1192
G1239
G1217(e)
G1207(g)
Reciprocal
G1047(a)
G1035(a)
(43)
(11)
(39)
(29)
x Solanum Rybinii
(23)
(52)
(72)
(3)
(28)
(31)
(39)
(80)
x S. Rybinii
G1395(a)
G1396
G1398(a)
G1399(a)
G1380
G1382
G1383
G1384
G1385(a)
G1386 & G1388
G1387
G1389

Fig . 2.

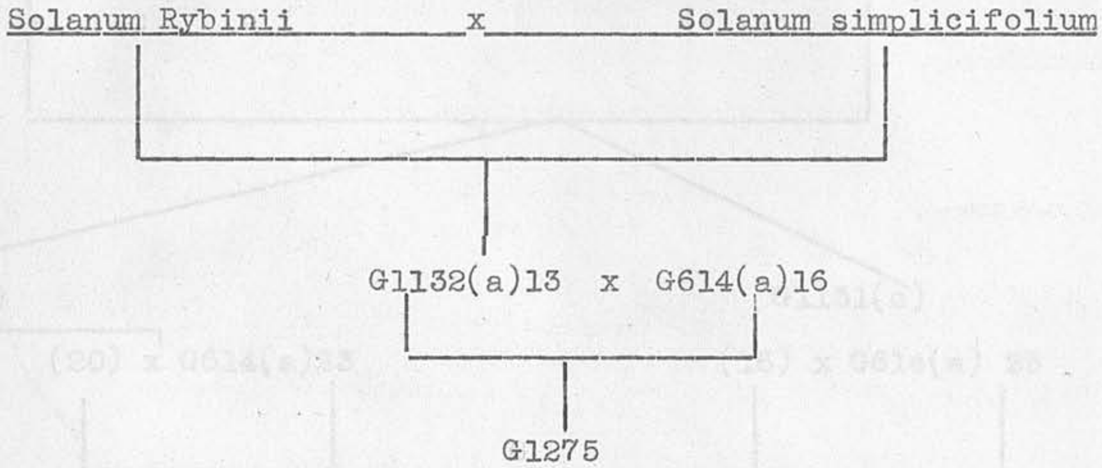

Solanum Rybinii x Solanum simplicifolium
G1132(a)13 x G614(a)16
G1275

Fig. 3.

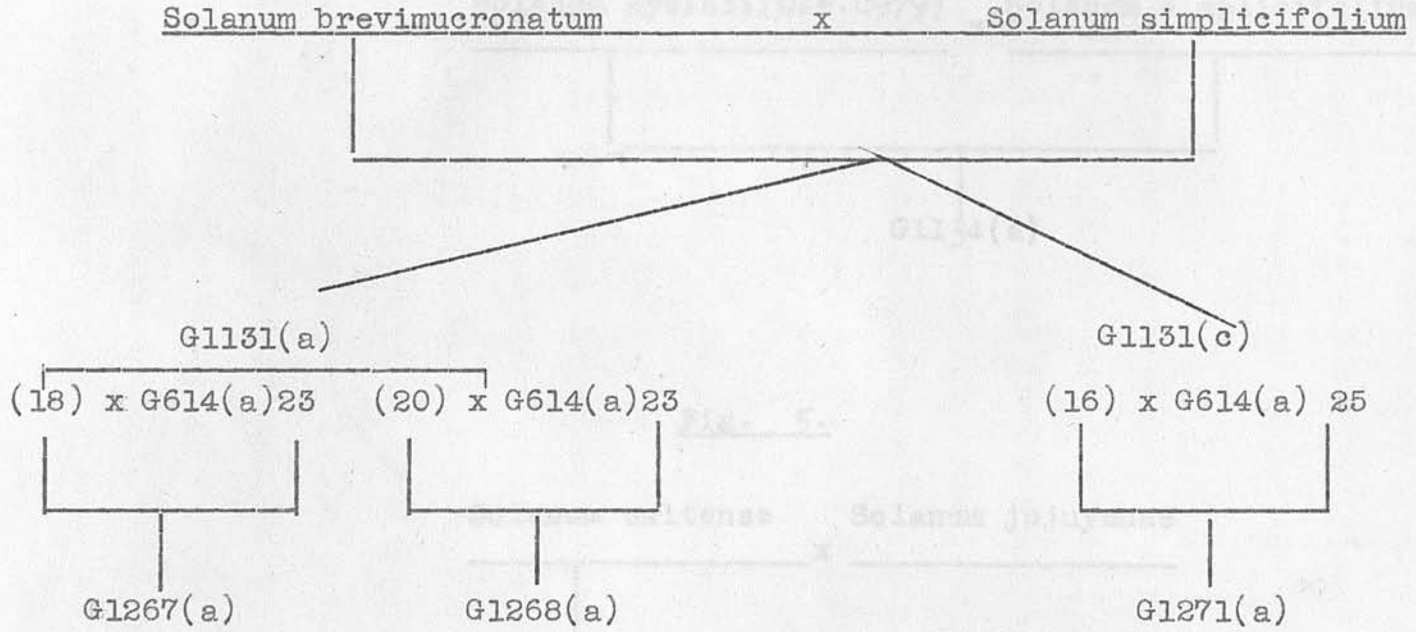

Solanum brevimucronatum x Solanum simplicifolium
G1131(a)
G1131(c)
(18) x G614(a)23
(20) x G614(a)23
(16) x G614(a) 25
G1267(a)
G1268(a)
G1271(a)

Fig. 4.

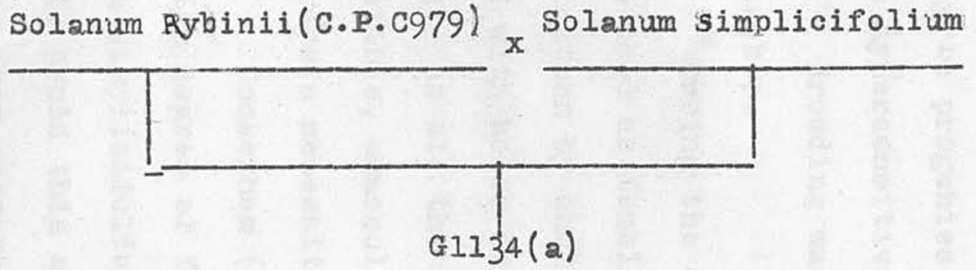
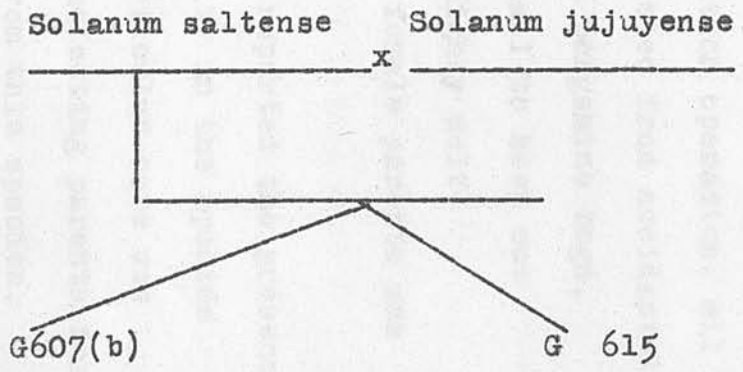

Solanum Rybinii(C.P.C979)
x
Solanum Simplicifolium
G1134(a)

Fig. 5.


Solanum saltense
x
Solanum jujuyense
G607(b)
G 615

Owing to a high degree of self-incompatibility throughout the Solanum Species used and their hybrid seedlings it was not possible to obtain seed by self-fertilisation. Consequently the available data refer entirely to progenies derived by cross fertilisation between hypersensitive and non-hypersensitive plants.

Breeding was done during the months of July to September.

During the cross pollination operation, all flowers used as females were protected from accidental contamination by enclosing them in pergamine bags, punched with holes sufficiently small to keep out insects. As all the plants were highly self-incompatible, emasculation of the female parents was not always a necessity.

Cockerham (unpubl.) has reported the presence of a high degree of female sterility in the species Solanum simplicifolium. Hence particular care was taken to avoid this sterility in selecting parents for breeding from progenies derived from this species. To facilitate the selection of seedlings for breeding, it was sometimes necessary to obtain preliminary information regarding their reactions to the viruses. For this purpose three leaves of each plant were inoculated with infective sap and the leaves were immediately detached from the plants at the base of the petiole. The detached leaves were then placed in water until the development of necrotic lesions on a proportion of them gave an indication of the plants which could be selected as hypersensitive parents in breeding More usually, progenies were raised for tuber production in the first year and prior to any testing for reactions to viruses, plants were crossed at random. Selection of seeds for further progeny testing was then made on the information obtained by testing the parents during the following year.

In raising material for testing, seeds of selected crosses were sown mostly in the year previous to the year of testing and tubers from the plants raised were collected and bagged separately in paper bags. During the following year the tubers were planted in pots in insect-proof glass-houses. Individual plants of each seedling were tested separately with each of the viruses. In the case of progenies which were examined for reaction to only one virus, the seedlings were tested as soon as possible after germination.

The varieties Arran Victory, Irish Chieftain, Craig's Defiance and Edgecote Purple were used as sources of viruses "X", "A", "Y" and "C" respectively. Although viruses "X" and "Y" occur in a number of relatively stable forms or strains, virus "X" used in this work was obtained entirely from a single infected clone of the variety, Arran Victory in which the virus causes mild mottle symptoms and virus "Y" was obtained from a single infected clone of the variety Craigs's Defiance, in which it is also a comparatively mild strain.

Infections were usually made by sap-inoculations except in the case of virus "A", where sap-inoculation proved unsatisfactory. All infections with virus "A", therefore, were made by grafting the seedlings under test with scions of Irish Chieftain containing virus "A". In the case of other viruses, sap was extracted from the leaves of the infector plants and mixed with phosphate buffer solution at pH.7 in equal proportions. The use of buffered sap not only added a measure of uniformity to inoculation but it also proved more satisfactory than unbuffered sap in producing necrotic symptoms on the infected leaves. Three leaves of each plant were dusted with carborandum powder (500 mesh) and infective sap was rubbed over the leaves with the help of a pestle and excess inoculation was then washed off with water. Sometimes pads made from cotton wool and cloth, or fingers were used for rubbing the sap on the leaves. Each infected leaf was marked for reference.

Plants infected by sap-inoculation showed symptoms of necrotic local lesions on the inoculated leaves within 7 to I0 days after inoculation. The plants showing no necrotic symptoms were reinoculated I4 days after the first inoculation.

Confirmation of the presence of virus "Y" and virus "C" in the infected plants was obtained by inoculating White Burley tobacco plants with sap from the potato plants under test, about 6 to 7 weeks after the first inoculation. If the virus was systemic in the potato plant, the inoculated tobacco plants showed vein-banding symptoms 7 to I0 days after inoculation. As an alternative to White Burley, a variety of Solanum demissum (C.P.C 2I67) was also used for the confirmation of the presence of virus "Y" and "C". Upon this host the appearance of necrotic local lesions on the inoculated leaves 4 to 5 days after rubbing with infective sap served to identify viruses "Y" or"C".

With virus "A" symptoms on potato seedlings appeared about I4 to 20 days after grafting. The identification of the necrotic symptoms on infected plants was made without difficulty, but in the absence of necrotic symptoms the scoring became quite difficult, because the plants did not always show any distinct mottling. Sometimes the Union of the Scion and the stock remained incomplete and the virus failed to enter the plants under test. Therefore, to be sure that the virus had entered and that the plants had become systemically infected, scions from all the plants showing no necrotic symptoms were grafted for the recovery of the virus, to the test varieties, Kerr's Pink or Craig's Defiance, which give hypersensitive reaction to virus "A". At a later stage of the investigation a variety of Solanum demissum , hypersensitive to virus "A", and capable of being infected by sap-inoculation was also used in the detection of systemic infections. Upon this host local necrotic lesions upon the inoculated leaves appear within 4 to 5 days instead of 18 to 30 days necessary for the appearance of top-necrosis in grafted Kerr's Pink or Craig's Defiance.

Serological tests were performed for the specific detection of virus "X" by a modification of the agglutination technique described by Van Slogteren (1943). Two drops of sap, extracted from the young leaves of each plant under test were put on a glass slide and mixed with a drop of anti-"X"- serum and 0·85 % saline solution respectively. The slide was examined under a microscope and the presence of virus "X" was detected by the agglutination reaction in the sap-antiserum mixture. The antiserum was prepared by Dr. Cockerham and Miss M^{c}Ghee at the Scottish Plant- Breeding Station.

In cases where persistent unsatisfactory results were obtained with any of the viruses, fresh tubers were planted and the plants were retested.

----------x---------

Experimental Results.

Segregation of Hypersensitive reaction to virus "X":-

Potato virus "X" was first described by Smith (I93I), although the virus has been recognised by different workers under different names and in combination with other viruses-

The only effective way of transmission of this virus in the field is, as reported by Loughnane and Murphy (I938), by means of leaf contact. Artificially the virus is transmitted by all kinds of sap-inoculation and by grafting. There is no evidence of any kind of insect vector for this virus.

In general the virus produces in the field various kinds of mosaic diseases in the potato varieties.

Top-necrotic reaction due to virus "X" was reported by Salaman and Bawden (I932) in the variety King Edward and later Bawden (I936) showed that the variety Arran Crest and Epicure also gave top-necrotic reactions following infection with virus "X", either by grafting or by needle inoculation. Cockerham (I937, I939. I943a,b,) and Cadman (I942) reported that potato plants, after being artificially infected with the virus by grafting reacted in one of the following ways. Either, (I) necrosis appeared in the shoot apices, showing typical top-necrotic symptoms. or, (2) mosaic symptoms of various intensities appeared in the leaves of the infected plants, or, (3) the plants showed no symptoms, ie, they were symptomless "carriers".

Cockerham (I943b) made an extensive study of the first type of reaction in a varied number of cultivated potato varieties and in some clones of wild species of potatoes (Cockerham I943 a). He reported that the symptoms observed, although variable between varieties, were essentially similar to those described by Quanjer (I93I) and Bawden (I932) under the name of "top-necrosis". In the above mentioned cases the plants were infected by grafting.

On the other hand Cockerham (I939) and Cadman (I942) reported that plants showing top-necrosis following infection with virus "X" by grafting usually reacted with necrotic local lesions when infection was carried out by sap-inoculation. Cockerham (I939) reported that in the necrotically reacting varieties, systemic infection by inoculation was not readily achieved, since there was a marked tendency for the virus to become localised at the point of infection.

In the seedling progenies used in the following investigation, a range of necrotic symptoms were obtained, following infection by sap-inoculation.

(I) These inoculated leaves showed local necrotic lesions and the plants did not become systemically infected, the virus being localised in the necrotic lesions.

(2) Necrotic local lesions appeared in the inoculated leaves, followed by a systemic necrosis resulting in the death of the whole plant, mostly from the top downwards.

(3) The inoculated leaves gave necrotic local lesions but the virus became systemic in the plants showing either mottle symptoms or no symptoms at all. Sometimes a few necrotic lesions were also obtained on the younger leaves.

(4) No necrotic symptoms appeared on the inoculated leaves but the virus became systemic, showing mottle symptoms or no symptoms at all. Tubers from the first group of plants were normal in appearance, plants raised from them were healthy, and no virus could be recovered from them. Usually no tubers were obtained from the second group of plants, but if tubers were obtained they were necrotic and either they failed to germinate or they produced small necrotic plants which died early. On the other hand the last two groups of plants produced tubers which gave rise to fully infected plants with either mottle symptoms or no visible symptoms of their infection.

When infections were made by graft transfers, the distinction between groups (I) and (2) disappeared, all the plants in both groups showing symptoms typical of top-necrosis and all eventually being killed. Plants in groups (3) and (4) however were never killed. They showed a wide variation in symptoms rang~~e~~ing from severe mosaics with necrotic flecks to evanescent mottles or they even showed no visible effects. The distinction between groups (I) and (2), on one hand, and groups (3) and (4), on the other hand was therefore well defined and sufficiently clear to classify plants of the first two groups as hypersensitive and of the third and fourth groups as non-hypersensitive.

Segregation data based on this classification are given in Tables I and 2. Hypersensitive plants concerned are Solanum brevimucronatum and Solanum jujuyense and three seedlings obtained from the cross between Solanum brevimucronatum and Solanum simplicifolium. In each case the cross is between a hypersensitive plant and a non-hypersensitive plant.

Table (1) shows that the F_1 progenies, G 1131(a) and G 1131(c) which were raised by crossing Solanum brevimucronatum with Solanum simplicifolium, segregated approximately in the ratio 1:1, hypersensitive to non-hypersensitive plants. Two other progenies G 615 and G 607(b) which were raised from the cross Solanum jujuyense X Solanum saltense and the reciprocal,

Table--1

F_1 progenies:--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			N x	n x	N x	n x	χ^2	D.F	P	
G1131(a)	S.brevimucronatum x S.simplicifolium	73	36	37	36.5	36.5	0.012	1	0.95 - 0.90	N n x x x n n x x
G1131(c)	Do.	29	16	13	14.5	14.5	0.31	1	0.70 - 0.50	Do.
G 615	S.jujuyense x S.saltense	23	11	12	11.5	11.5	0.042	1	0.70 - 0.50	Do.
G 607(b)	S.saltense x S.jujuyense	35	17	18	17.5	17.5	0.028	1	0.90 - 0.80	n n x x x N n x x
Total		160	80	80	80	80	0.770	4		

χ^2 Calculated on the Totals = 0
D.F = 1

Heterogeneity = 0.770
D.F = 3 ; P = 0.90 - 0.81

Table--2

F_1 x recessive progenies :—

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			N_x	n_x	N_x	n_x	χ^2	D.F	P	
G1267(a)	G1131(a)18 x G614(a)23	47	22	25	23.5	23.5	0.19	1	0.70 - 0.50	$N_x n_x$ x $n_x n_x$
G1268(a)	G1131(a)20 x G614(a)23	21	10	11	10.5	10.5	0.046	1	0.90 - 0.80	Do.
G1272(a)	G1131(c)16 x G614(a)25	83	40	43	41.5	41.5	0.108	1	0.80 - 0.70	Do.
Total		151	72	79	75.5	75.5	0.344	3		

χ^2 Calculated on the totals = 0.324

D.F= 1 ; P - 0.70-0.50

Heterogeneity = 0.02

D.F. = 2 ; P = 0.99 - 0.98

also gave approximately 1:1 ratio.

Hypersensitive plants from the progenies G 1131(a) and G 1131(c) were selected and the progenies G 1267(a), G 1268(a) and G 1272(a) were obtained by crossing those hypersensitive plants with non-hypersensitive plants selected from the progeny G 614(a) (Fig.1.). The progenies raised from these F_1 (hypersensitive) X non-hypersensitive crosses were tested with virus "X" and table (2) shows that in every case the ratio obtained for hypersensitive to non-hypersensitive plants is approximately 1:1.

The data obtained from Tables 1 and 2 show,

(1) that the segregation is of 1:1 ratio throughout all the progenies,

(2) that there is a similarity in segregation between Solanum brevimucronatum and Solanum jujuyense,

(3) that there is a similarity in segregation between the reciprocal crosses,

(4) that there is a similarity in segregation between the parents and offsprings.

These results suggest that as in tetraploid material a single gene is concerned with the manifestation of hypersensitive reaction to virus 'X' in these plants and that the mode of inheritance is simple.

----------X----------

Segregation of Hypersensitive reaction to virus "A":-

Virus "A" has been described as an individual virus by Murphy and M^{c}Kay (I932) in the variety Irish Chieftain. But the virus was previously described by Salaman (I930) and Murphy and M^{c}Kay (I93I), as a component of the "crinkle" disease of potatoes. This virus alone produces in some varieties of potatoes, a type of mottling symptom, but along with virus "X" it produces severe "crinkle" disease (Murphy and M^{c}Kay, I932). It is transmitted in the field by the aphis, Myzus persicae but it is not transmitted by contact. It is very difficult to transmit the virus, artificially by sap-inoculation except to White Burley tobacco plants (Laughnane I933,Clinch and Laughnane I933). Only one variety of Solanum demiss~~i~~um proved to be easily infected by sap-inoculation showing necrotic symptoms.

Although in many reactions it resembles potato virus "X", the absence of any immunological relationship between the two indicates their separate identities. (Smith I937 text)

virus A

Schültz (I925) reported that the variety Duke of York, when grafted with scions from the variety American Green Mountain gave a reaction similar to that which was later named "top-necrosis." From later evidence it seems probable that the reaction observed was due to virus "A" (Dykstra I939;,Cockerham I943b). Hence, this seems to be the first record of "top-necrosis."

due to virus "A". Such reactions were also obtained by Salaman (1930) in the vari~~a~~ety Great Scott, by Murphy and McKay (1932), and by Clinch and Loughnane (1933) in Up-to-date and British Queen.

Cockerham (1937, 1939) showed that when cultivated varieties of potatoes were grafted with scions containing virus "A", the plants either reacted with top-necrosis or non-necrotic types of symptoms. Later Cockerham (1943ab) reported that top-necrotic symptoms due to virus "A" differed from that of the top-necrotic symptoms due to virus "X", in the expression of initial symptoms; although the ultimate effect was the same. He found that in the cultivated varieties showing top-necrosis, the symptoms first appeared on the young expanded leaves above the graft union as yellow blotchy mottles which rapidly gave place to large patches of necrotic tissue. Necrotic lesions also appeared at the shoot apex and gradually the whole plant collapsed due to the spread of necrosis. He also reported another restricted type of top-necrotic symptom in the varieties, Epicure, Great Scot etc, where symptoms first appeared as small necrotic spots immediately under the terminal bud. Sometimes the necrosis did not spread any more and the rest of the shoot grew normally; but mostly the necrosis spread upwards into terminal buds resulting in a type of restricted "top-necrosis", which Cockerham named "Apical top-necrosis".

The above mentioned symptoms are all of a hypersensitive nature.

In the seedling progenies tested in this work with virus "A" by graft infection, symptoms appeared first in the apical leaves of the terminal shoots. Gradually all the shoots collapsed from top downwards due to the spread of the necrosis resulting in the death of the whole plant. There seems to be no evidence of "apical top-necrosis" in the seedling progenies under consideration. The non-hypersensitive plants either showed mottling or became "carriers".

All the progenies tested with virus "A" were raised from initial material of 24-chromosome Solanum species, Solanum simplicifolium, Solanum brevimucronatum, Solanum saltense, Solanum jujuyense and Solanum Rybinii, and Figs.I to 5 show the family trees of the progenies tested with the virus.

All the plants were infected by grafting with scions from the variety Irish Chieftain, containing virus "A"-

The presence of hypersensitive reaction to virus "A" in Solanum simplicifolium and Solanum saltense was first obtained by Cockerham (I943 a).

Solanum brevimucronatum, Solanum jujuyense, and Solanum Rybinii on the other hand gave non-hypersensitive reaction.

The work was started by Dr. Cockerham to study the segregation of the hypersensitive reaction. to virus "A", "Y" and "C" in the progenies raised from the cross; Solanum simplicifolium x Solanum Rybinii. He pointed out, however, that the genetic situation was obscure. This obscurity arose from the fact that in the progeny G614 (a) derived from Solanum simplicifolium used as female parent, anomalous segregation ratios were obtained. The ratio of hypersensitive to non-hypersensitive plants obtained by Dr. Cockerham in the progeny G614 (a) was approximately 7:1. Furthermore, in that progeny exactly similar segregation data were obtained with virus "Y" and virus "C", the four non-necrotic plants in each case being identical.

These results called for further investigation, firstly to determine the cause of the anomalies in the segregation and secondly to examine the possibility that a single genetic unit controlled reaction to the viruses "A", "Y" and "C".

The first step in this investigation was taken by examining the progeny G1132(a), derived from the reciprocal cross, Solanum Rybinii x Solanum simplicifolium. As will be seen in table 3, the segregation obtained in the progeny G1132(a) was 47 necrotic to 48 non-necrotic or approximately a ratio of 1:1. Moreover the progeny G1131(a) and G1131(c) which were derived from the cross, Solanum brevimucronatum x Solanum simplicifolium also gave approximately I:I ratio of hypersensitive to non-hypersensitive plants.

It,is clear, therefore, that the anomalous segregation occurs only when Solanum simplicifolium is used as a female parent. Evidence throwing some light on the situation has been provided by Cockerham (unpubl) who has found that Solanum simplicifolium carries genetic factors for female sterility and is itself partially female sterile. The investigation of these factors is, however, insufficiently far advanced to offer a complete explanation of their relationships to the genes controlling reaction to viruses "A", "Y" and "C". In order to avoid further anomalies all the material used in the present studies has been selected with due regard to the presence of female sterility in progenies derived from Solanum simplicifolium. This has been accomplished in three ways. Firstly, by direct reference to Cockerham's data; secondly by the use as male parents only of seedlings carrying female sterility factors; and thirdly, by the rejection of all material which through the presence of a proportion of infertile seed, gave indication of having been derived from a partially sterile female plant.

Now, table 3, shows that two more progenies G607(b) and G6I5, which were derived from the cross, Solanum saltense x Solanum jujuyense and its reciprocal cross, also gave approximately I:I ratio of hypersensitive to non-hypersensirive plants. Hence I:I ratio obtained in the F_I,progenies, raised from

Table--3

F_1 progenies:-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			N_A	n_a	N_A	n_a	χ^2	D.F	P	
G1132(a)	S. Rybinii x S. simplicifolium	95	47	48	47·5	47·5	0·01	1	0·95-0·90	$n_a\ n_a$ x $N_A\ n_a$
G1131(a)	S. brevimucronatum x S. simplicifolium	74	39	35	37	37	0·216	1	0·70-0·50	Do.
G1131(c)	Do.	30	15	15	15	15	0	1		Do.
G 607(b)	S. saltense x S. jujuyense	35	18	17	17·5	17·5	0·028	1	0·90-0·80	$N_a\ n_a$ x $n_a\ n_a$
G 615	S. jujuyense x S. saltense	22	12	10	11	11	0·09	1	0·80-0·70	$n_a\ n_a$ x $N_A\ n_a$
Total		256	131	125	128	128	0·344	5		

χ^2 Calculated on the totals = 0·14
D.F = 1 ; P = 0·80 - 0·70

Heterogeneity = 0·204
D.F = 4 ; P = 0·99

Table--4

F_1 intercrossed progenies:-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			$\genfrac{}{}{0pt}{}{N}{A}$	$\genfrac{}{}{0pt}{}{n}{a}$	$\genfrac{}{}{0pt}{}{N}{A}$	$\genfrac{}{}{0pt}{}{n}{a}$	χ^2	D.F	P	
G1192	G 614(a) 3 X G 614(a) 7	50	36	14	37.5	12.5	0.215	1	0.70 - 0.50	$\genfrac{}{}{0pt}{}{N\ n}{A\ a} \times \genfrac{}{}{0pt}{}{N\ n}{A\ a}$
G1272(a)	G1131(c) 16 x G 614(a) 25	62	35	27	31	31	1.032	1	0.50 - 0.30	$\genfrac{}{}{0pt}{}{N\ n}{A\ a} \times \genfrac{}{}{0pt}{}{n\ n}{a\ a}$
G1268(a)	G1131(a) 20 x G 614(a) 23	21	12	9	10.5	10.5	0.428	1	0.70 - 0.50	Do.
G1217(e)	G 614(a) 24 x G614(a) 10	13	5	8	6.5	6.5	0.692	1	0.50 - 0.30	Do.
G1267(a)	G1131(a) 18 x G 614(a) 23	37	0	37	0	37	0	1		$\genfrac{}{}{0pt}{}{n\ n}{a\ a} \times \genfrac{}{}{0pt}{}{n\ n}{a\ a}$

the crosses between hypersensitive and non-hypersensitive plants has been confirmed.

Table 4 shows that the progeny, GII92, which was raised by intercrossing two hypersensitive plants selected from the F_I, progenies, G6I4(a), gave approximately 3:I ratio, of hypersensitive to non-hypersensitive plants. The other three progenies GI272(a) GI268(a) and GI2I7(e) which was raised by crossing the hypersensitive plants selected from F_I, progenies with non-hypersensitive plants, gave approximately I:I ratio and in the progeny GI267(a) raised by intercrossing two non-hypersensitive plants, 0:∞ ratio was obtained.

Cadman (I942) and Cockerham (I943b) have reported that hypersensitive reaction to virus "A", in the cultivated varieties of potatoes was conditioned by a single dominant gene, N_A.

From the results of tables 3 and 4, it seems evident that in these 24-chromosome potatoes, also, the hypersensitive reaction to virus "A" is controlled by a single dominant gene.

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Linkage between the genes N_X and N_A.

A close linkage between the genes N_X and N_A, responsible for the hypersensitive reaction to viruses "X" and "A"., in the cultivated varieties of potatoes has already been established by Cadman (1942) and Cockerham (1943a, 1945).

In the work also attempts have been made to investigate the interrelationship between the two genes in the 24-chromosome potatoes.

As no 24-chromosome potato species hypersensitive to both viruses was available, material containing both the dominant genes was synthesised by crossing Solanum brevimucronatum with Solanum simplicifolium and Solanum jujuyense with Solanum saltense. Solanum brevimucronatum and Solanum jujuyense are hypersensitive to virus "X" and Solanum simplicifolium and Solanum saltense are hypersensitive to virus "A".

Each plant of these F_1, progenies was tested with both the viruses "X" and "A" and four sets of plants were obtained, eg. (1) plants hypersensitive to both viruses, (2) plants hypersensitive to virus "X" only. (3) plants hypersensitive to virus "A" only and (4) plants non-hypersensitive to both the viruses.

Now, it has already been shown in the previous chapters that each of these 24-chromosome potato species was heterozygous for a single dominant gene; in one set of species the dominant gene being N_X and in the other set it being the gene N_A. Hence the first set of plants of the F_1 progenies were heterozygous for two dominant genes, each of them coming from two different parents, and the information on the linkage between the two genes in the repulsion phase could be obtained by back-crossing these plants.

Therefore, the plants hypersensitive to both the viruses were selected from the F_1 progenies and attempts were made to cross them with non-hypersensitive plants. Succesful fertilisations were obtained only in the F_1 progenies raised from the cross, Solanum brevimucronatum x Solanum simplicifolium . Seedlings raised from the cross Solanum jujuyense x Solanum saltense failed to flower in each of two seasons, and it was not possible, therefore, to continue further intended experiments with material from this source.

In order to obtain the information on the linkage in the repulsion phase between the genes conditioning the hypersensitive responses, each plant of the progenies raised from the backcrosses with the recessive plants, was tested with viruses "X" and "A". The information on the linkage was obtained from the value of the frequency of recombinations, ie., from the total number of the plants hypersensitive or non-hypersensitive to both the viruses.

Now, the information on the linkage between the genes in the coupling phase could be obtained by crossing the plants of the back-cross progenies, carrying both the dominant genes, with recessive plants. Hence attempts were made to select those plants from the back-cross progenies and to cross them with recessive plants. But, as the breeding was to be done in the year previous to the year in which the plants were tested and none of the plants from which the crosses were made proved to be hypersensitive to both the viruses, it was not possible to obtain any information on the linkage between the genes in the coupling phase. Moreover, it has been shown in the following data that the linkage between the genes in the repulsion phase is very strong. Hence, the chances of occurence of the plants with both the dominant genes in the back-cross progenies was very little.

Detection of Linkage.

For the detection of linkage, data from two progenies, G I268(a) and G I272(a) have been analysed by the χ^2 method (Mather I938 text) as in Table 5.

The basis of the analysis is that, since

Table--5

Progenies	Frequency of Combination				Total	Components of χ^2			
	XA	Xa	xA	xa		X,x	A,a	Linkage	D.F.
G1268(a)	1	9	11	0	21	0.047	0.428	17.1904	1
G1272(a)	3	27	32	0	62	0.064	1.031	50.5829	1
Total	4	36	43	0	83	0.111	1.460	67.7733	2

Table--6.

Gene Pair	Total	Deviation		Heterogeneity		
	χ^2	P	D.F	χ^2	P	D.F
X,x	0·108	0·8 - 0·7	1	0·003	0·98-0·95	1
A,a	1·47	0·3 - 0·2	1	0·990	0·5 - 0·3	1
Linkage	67·7710	less than 0·001	1	0·0023	0·98-0·95	1

$\therefore \chi^2_L = 67 \cdot 710$; $P =$ less than 0·001 both families are derived from heterozygotes crossed with recessives, independent segregation should show an equal number of segregates in the four groups,

(1) plants hypersensitive to both the viruses "X" and "A".

(2) plants hypersensitive to virus "X" only,

(3) plants hypersensizive to virus "A" only and

(4) plants non-hypersensitive to both the viruses-

χ^2 is partitioned into three components, two of which are concerned with the deviation of the single genes from the expected ratios and the third one with detecting association of the two genes in segregation; the expectation being that the genes are independent in segregation.

In table 5, the deviation from expectation has been shown for each of the individual progenies and in table 6, for the totals. χ^2 of the component of linkage for one degree of freedom in each of the progenies segregating for the genes N_X and N_A is very large and the χ^2 of the component of linkage for one degree of freedom calculated on the totals of both the progenies is also very large; the value of P (probability) being very small.

The heterogeniety of each component between the progenies has been tested and it shows in Table 6 that it is not significent in any of the cases.

Hence, these results show that the two

families agree significantly in showing that the segregations of the genes concerned are not independent. Hence, it can be concluded that the two genes concerned are linked.

Estimation of Linkage.

In "diploids" the linkage is measured by the frequency of recombination gametes; since these are the direct indication of the frequency of recombination chromatids. As each of the dominant genes has come from different parents, the linkage between the two genes in these two progenies is in the repulsion phase and the value of the frequency of recombination (p) has been calculated on the formula $p = \frac{a_I + a_4}{n}$ (a_I, a_2, a_3 and a_4 representing the frequencies of the four combinations, a_I and a_4 being the new combinations XA and xa, and n being the total number of plants). (Mather I938 text).

Table 7 shows the linkage value, in each of the progenies and also of the totals of the progenies. From the results it shows that the recombination value is of the order of 4·8%, a value suggesting an extremely strong linkage.

Hence, from the above investigations, the following conclusions can be drawn:--

(I) that the two families are homogeneous,

(2) that in each family there is no agreement with the hypothesis of independent segregation of the

Table--7

Progenies	Frequency of combination				Total	Linkage Value	Standard Error
	XA	Xa	xA	xa			
G 1268(a)	1	9	11	0	21	4.7 %	± 4.6 %
G 1272(a)	3	27	32	0	62	4.8 %	± 2.7 %
Total	4	36	43	0	83	4.8 %	± 2.3 %

two genes concerned,

(3) that the genes are linked in the repulsion phase, and

(4) that the linkage in the repulsion phase is very close.

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Segregation of hypersensitive reaction to virus 'Y'

Virus 'Y' (Smith 1931) has been described according to many of its characteristic symptoms on different host plants under the names "Streak" (Orton 1920), "Leaf-drop-streak" (Murphy 1921), "Stipple streak" (Atanasoff 1922) and "vein banding" virus (Valleau and Johnson 1930).

The virus is transmitted in the field by aphis vectors principally by Myzus persicae Sütz and it can readily be transmitted artificially by sap inoculation and by grafting.

Evidence of hypersensitive reaction to virus 'Y' in cultivated varieties of potatoes has been reported by Hutton and Bald (1944, 1945 a.b) and in certain South American species and varieties of potatoes by Cockerham (1943 a.b, 1946, 1947). The latter author has reported lethal necrotic reactions to infection in the "diploid" species, Solanum simplicifolium, in two clones ofthe "pentaploid" species, Solanum Salamanii and in two clones of the "hexaploid" species, Solanum demissum.

The initial material which was used for breeding during the following experiment were the "diploid" (2n=24) species, Solanum simplicifolium (C.P.C 51 A), Solanum brevimucronatum (C.P.C 71) and two varieties of Solanum Rybinii (C.P.C 1311 and C.P.C 979). Solanum simplicifolium reacted with hypersensitive reaction following infection with virus 'Y', while Solanum brevimucronatum, and both the varieties of the Solanum Rybinii gave non-hypersensitive reaction with the virus. Figs. 1, 2 and 3 shows the family tree of the crosses made and the progenies tested.

Virus 'y' has been reported to exist in a number of different strains, which differ in the type and severity of symptoms they induce in potato varieties (Solaman 1937; Köhler 1937; Nobrega and Silberschmidt 1944, and Bawden and Kassanis 1947). and virus 'C' has been confirmed to be a strain of virus 'Y' (Cockerham 1943 a; Bawden & Sheffield 1944 and Hutton 1946). In order to study the difference in hypersensitive reaction due to different strains of virus 'Y' two plants of the "diploid" species, Solanum simplicifolium were infected with each of four different strains of virus 'Y'; three of which namely, Sheffield-'Y', Rothamsted-'Y' and 18·2-'Y', were obtained from the Rothamsted Experimental Station and the fourth one was the ordinary strain of virus 'Y' obtained from the variety Craig's Defiance.

Table - 8 shows that with all the four strains of virus 'Y' Solanum simplicifolium showed hypersensitive reaction. With the first two strains (Sheffield-'Y'

Table. 8.

Species	Strains of Virus 'Y'	Symptoms obtained
Solanum simplicifolium	Sheffield 'Y'	Very distinct necrotic local lesions and few veinal necrotic lesions appeared on the inoculated leaves but the virus did not become systemic. No mottling was present and virus could not be recovered from the young leaves
	Rothamsted 'Y'	Do.
	18.2- 'Y'	Necrotic local lesions appeared on inoculated leaves followed by systemic necrosis resulting in the death of the whole plant.
	C.D.- 'Y'	Do.

and Rothamsted-'Y') the plants gave only local lesions, while with the other two strains the plants gave a systemic necrotic lethal reaction. Hence it seems evident that Solanum simplicifolium is hypersensitive to four strains of virus 'Y'.

During the following experiment the strain of virus 'Y' which was obtained from the variety Craig s Defiance was used as a source of infection and all the plants were infected by sap-inoculation.

In the hypbrid seedling progenies the classification of plants showing hypersensitive and non-hypersensitive reactions became very difficult owing to a range of necrotic symptoms which appeared in them. According to the first symptoms shown, plants can be classified primarily into two main groups:- (A) plants showing necrotic local lesions on the inoculated leaves and, (B) plants showing no necrotic local lesions on the inoculated leaves. Later the plants showing necrotic local lesions behaved in one of the following ways; viz: (1) the virus did not become systemic and remained restricted in the necrotic lesions, (2) the necrosis became systemic resulting in the death of the plants, (3) the virus became systemic showing few necrotic lesions or streaks on the non-inoculated leaves and the virus was recovered from the younger leaves, (4) the virus became systemic without showing any systemic necrotic symptoms; but sometimes mottle symptoms were present. In the last two groups of plants the necrotic symptoms on the inoculated leaves were mostly very inconspicuous and mostly in the form of streaks.

Among the plants showing no necrotic local lesions, the plants were systemically infected and showed either, (1) mottle symptoms or (2) no symptoms at all ie. they were symptomless"carriers".

In the case of virus 'Y' as in the case of virus 'X', the first two groups of plants among the necrotic plants seems to be of hypersensitive types; hypersensitiveness being shown in the death of local tissue at the site of the virus entry in the first group of plants and in the death of the whole plant in the second group of plants. In this case also both the groups of plants reacted with the same lethal reaction when the infection was done by grafting, while in the case of other groups of plants non-lethal systemic symptoms were obtained following infection by grafting. Therefore, symptoms obtained in the first two groups of plants among the necrotic groups were classified as of hypersensitive types and the rest of the plants as of non-hypersensitive types.

Cadman (1942) suggested that different manifestations of the lethal necrotic reactions to the viruses 'X', 'A', 'B' and 'C' might be due to the quantity of virus entering the plants at infection.

During these experiments it has been experienced along with Hutton (1945) that the expression of hypersensitive reaction varied with the time of the year in which the plants were tested and with their physiological conditions at infection.

To obtain a very general idea about the relationship between the growth of the plants and the impression of hypersensitive reactions, six tubers were selected from each of the several plants, which gave hypersensitive reaction to virus 'Y' during the previous year. These six tubers were divided into three groups of two tubers each and the plants from them were inoculated at three different stages of growth, as, (1) when the plants were very young, (2) when the plants had just started flowering and (3) when flowering was over.

Though no definite conclusion could be reached, indication was obtained from these inoculations that the older the plants at the time of inoculation, the fewer was the necrotic lesions obtained on the inoculated leaves. In fact, at the late stage of growth it became quite difficult to infect the plants by inoculation. During the current year's test, only one plant reacted with systemic lethal necrosis, a plant which was infected at the early stage of growth.

This work was started by Dr. Cockerham. In his study of the behaviour of potato species and varieties to infection with viruses, Cockerham (1943) reported violent necrotic reactions to graft infection with virus 'Y' in the "diploid" species Solanum simplicifolium. Later (Cockerham 1946, 1947) ~~he~~ showed that the reaction was inherited and that many seedlings possessing the character were hypersensitive to and field-immune from the virus under natural spread of infection. He pointed out however, that the genetical situation was obscure. This obscurity arose from the fact that in the early progenies, ~~are~~ derived from Solanum simplicifolium used as a female parent, anomalous segregation ratios were obtained. In three small progenies raised from the cross Solanum simplicifolium X Solanum Rybinii, for example, segregations of 29 necrotic to 4 non-necrotic; 6 necrotic to 1 non-necrotic and 20 necrotic to 3 non-necrotic plants were obtained. Furthermore, in one progeny, G 614 (a), exactly similar data were obtained with virus 'A' and virus 'C', the four non-necrotic plants in each case being identical.

As reported in the case of virus 'A', these results called for further investigation firstly to determine the cause of the anomalies in the segregation and secondly to examine the possibility that a single genetic unit controlled reactions to the three viruses 'Y', 'C' and 'A'.

The investigation was begun by examining

Table--9

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			N Y	n y	N Y	n y	χ^2	D.F	P	
G1174(b)	S. simplicifolium x S. Rybinii	37	28	9	18·5	18·5	9·6	1	0·01-0·001	N n x n n Y y y y
G1132(a)	S. Rybinii x S. simplicifolium	99	49	50	49·5	49·5	·01	1	0·9-0·8	n n x N n y y Y y
G1131(a)	S.brevimucronatum x S. simplicifolium	75	35	40	37·5	37·5	·32	1	0·7-0·5	n n x N n y y Y y
G1131(c)	Do.	30	16	14	15	15	·12	1	0·7-0·5	Do.
G1134(a)	C.P.C. 979 x *S. simplicifolium*	19	11	8	9·5	9·5	·46	1	0·5-0·3	Do.

for reactions to virus 'Y', a further progeny derived from the cross, Solanum simplicifolium X Solanum Rybinii {G 1174 (b)} and also a progeny derived from the reciprocal cross, Solanum Rybinii X Solanum simplicifolium, {G 1132(a)}. As will be seen in Table 9, the segregation obtained in the progenies were 28 necrotic to 9 non-necrotic or approximately a ratio of 3:1 in the progeny G 1174 (a) and 49 necrotic to 50 non-necrotic in the progeny of the reciprocal cross G 1132(a). In this case also, it is clear, therefore, that the anomalous segregations occurs only when Solanum simplicifolium is used as a female parent. Two other progenies, G 1131(a) and G 1131(c) which were raised from the cross, Solanum brevimucronatum X Solanum simplicifolium using Solanum simplicifolium as a pollen parent in both the crosses, also gave approximately 1:1 ratio (Table 9). Hence, the same explanation also can be put forward, as it was done in the case of virus 'A', to explain the anomalies in segregations obtained by Dr. Cockerham, and 1:1 ratio of hypersensitive to non-hypersensitive plants is also confirmed in this case for the segregation of the F_1, progenies. The same care was taken, as it was done in the case of virus 'A', to avoid further anomalies by selecting all the material used in the present studies with due regard to the presence of female sterility in the progenies derived from Solanum simplicifolium.

But this result does not provide any conclusive information about the nature of inheritance of the gene N_y and the genetic constitution of the plants concerned. Because, with respect to a single pair of allels Aa, simplex autotetraploid (Aaaa), simplex allotetraploid ($A_1a_1a_2a_2$) and heterozygous diploid (Aa) when backcrossed gives in each case 1:1 ratio for dominants to recessives.

Attempts were, therefore, made to throw some light on the nature of inheritance of the gene controlling hypersensitive reaction to virus 'Y'.

Disomic and tetrasomic inheritance can be distinguished by the following tests.

Selfing a simplex genotype, in all the three above mentioned cases, a 3:1 ratio of dominants to recessives is expected. But in the disomic case one third of the individuals in the dominant class will be homozygous, ie, they will not segregate again; while in the tetrasomic case non-segregators will be very rare or absent.

Due to complete self-incompatibility, selfing of the plants was not possible. Hence hypersensitive plants of the F_1, progenies were selected, and they were intercrossed.

Table 10 shows that segregation in the progenies G 1035(a), G 1047(a) and G 1207(g) which were

Table--10

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			NY	n_y	NY	n_y	χ^2	D.F	P	
G1035(a)	G 614(a) 7 x G 614(a) 8	100	72	28	75	25	·48	1	0·5 - 0·3	NY n_y x N_y n_y
G1047(a)	G 614(a) 8 x G 614(a) 7	44	31	13	33	11	·48	1	0·5 - 0·3	Do.
G1207(g)	G 614(a) 33 x G 614(a) 17	45	34	11	33·75	11·25	·006	1	0·95 - 0·9	Do.
G1225(f)	G 614(a) 11 x G 614(a) 16	50	26	24	25	25	·08	1	0·8 - 0·7	NY n_y x n_y n_y

Table--11.

Progenies	Parents	Total	Observed		Expected		Deviation			Suggested Genotype
			N_Y	n_y	N_Y	n_y	χ^2	D.F	P	
G1380	G1035(a) 23 x S. Rybinii	56	56	0	56	0	0	1		$N_Y N_Y$ x $n_y n_y$
G1386	G1035(a) 31 x S. Rybinii	59	59	0	59	0	0	1		Do.
G1388	G1035(a) 31 x S. Rybinii	101	101	0	101	0	0	1		Do.
G1382	G1035(a) 52 x S. Rybinii	62	32	30	31	31	·06	1	0·9 - 0·8	$N_Y n_y$ x $n_y n_y$
G1383	G 1035(a) 72 x S. Rybinii	60	29	31	30	30	·06	1	0·9 - 0·8	Do.
G1384	G1035(a) 3 x S. Rybinii	36	18	18	18	18	0	1		Do.
G1385	G1035(a) 28 x S. Rybinii	69	31	38	34·5	34·5	·71	1	0·5 - 0·3	Do.
G1387	G1035(a) 39 x S. Rybinii	64	31	33	32	32	·06	1	0·9 - 0·8	Do.
G1389	G1035(a) 80 x S. Rybinii	50	23	27	25	25	·32	1	0·7 - 0·5	Do.
G1395(a)	G1047(a) 43 x S. Rybinii	106	56	50	53	53	·32	1	0·7 - 0·5	Do.
G1396	G1047(a) 11 x S. Rybinii	44	24	20	22	22	·36	1	0·7 - 0·5	Do.
G1398(a)	G1047(a) 39 x S. Rybinii	115	55	60	57·5	57·5	·21	1	0·7 - 0·5	Do.
G1399(a)	G1047(a) 29 x S. Rybinii	64	34	30	32	32	·24	1	0·7 - 0·5	Do.

raised by intercrossing hypersensitive plants selected from the progeny G 614(a), occurred approximately in the ratio of 3 hypersensitive to one non-hypersensitive. One of the hypersensitive plants G 614(a) 11 was crossed with a non-hypersensitive, plant and Table 10 shows that the progeny, G 1225(f) raised from that cross segregated approximately in the ratio 1:1.

To test for the non-segregating or homozygous plants in the intercrossed progenies, plants showing hypersensitive reactions were selected from the progenies G 1035(a) and G 1047(a) and crossed with Solanum Rybinii (C.P.C.1311).

Thirteen progenies from those crosses were raised and tested with virus 'Y'. Table 11 shows that three of those thirteen progenies, namely G 1380, G 1386 and G 1388 showed no segregation at all and the rest of the progenies gave approximately 1:1 ratio in each case.

Therefore three out of thirteen progenies tested, showed no segregation which is quite compatible with the expectation in the disomic type of inheritance. Moreover from the results of Tables 8 and 9 it seems quite clear that in the initial material, the hypersensitive reaction is conditioned by the presence of a single dominant gene, which may be designated as N_y. The individual hypersensitive plants in the F_1 progeny, G 614(a), therefore, have a single dominant gene only.

Now, the plants in the progenies G 1035(a) and G 1047(a), which were synthesised by intercrossing the dominant plants from the F_1, progenies cannot have more than two dominant genes, which again came from the same source, Solanum simplicifolium. Hence the two non-segregating progenies are homozygous for two dominant genes.

From these results it can be concluded that the hypersensitive reaction to virus "Y" in these 24-chromosome potato species is controlled by a single dominant gene N_Y and that the inheritance in these 24-chromosome potato species is of disomic type with respect to the gene N_y.

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Segregation of Hypersensitive Reaction to virus 'C'.

Salaman first described a virus, carried in the variety Di Vernon, which caused "top-necrosis" in the variety President but not in Arran Victory. Quanjer (1931) also found the same virus in the variety Monocroat. This virus was later described and designated as virus 'C' by Bawden (1936), who also reported that in Di Vernon the virus was accompanied by viruses 'X' and 'Y' and in Monocroat by virus 'X'. Later the virus was described in greater detail by Cockerham (1943a) who found it free from viruses 'X', 'A', 'B' and 'Y' in Edgecote Purple and in a number of old British varieties.

Virus 'C' is artificially transmitted by sap inoculation and by grafting. Failure to transmit the virus by aphids was reported by Cockerham (1943b) and Bawden and Sheffield (1944). But Cockerham (1943a) reported that potato seedlings growing in the vicinity of infected Edgecote Purple became infected with virus 'C'. Similarly Bawden and Kassanis (1947) found Majestic plants growing near infected Di Vernon and Dargill Early to be naturally infected with virus 'C'. They remarked that "occasional individual of Myzus persicae or other potato aphids may be vector, but it is only a rare colonizer of potatoes".

In tobacco plants the symptoms produced

by virus 'C' are very similar to those produced by virus 'Y'.

Virus 'C' was first suggested to be a strain of virus 'Y' by Cockerham (1943b) and confirmed as such by Bawden and Sheffield (1944, 1947) and Hutton (1946).

Hypersensitive reaction in cultivated potatoes following infection with virus 'C' by grafting has been described in detail by Cadman (1942) and Cockerham (1943a b). They established that the top-necrotic reaction to virus 'C' in the cultivated potato varieties is conditioned by a single dominant gene, which they designated as N_C.

Hutton (1946) also reported the presence of hypersensitive reaction with virus 'C' in seedling progenies, raised from crosses between some cultivated varieties of potatoes.

The presence of hypersensitive reaction to virus 'C' in the "diploid" species Solanum simplicifolium was obtained by Cockerham (1943a) and Solanum brevimucronatum and Solanum Rybinii were found to give non-hypersensitive reaction to the virus.

The material for the following experiments was initially raised from the parents Solanum simplicifolium, Solanum brevimucronatum and Solanum Rybinii; and Figs. 1, 2 and 3 gives the family tree of the progenies tested.

All the plants were infected by sap inoculation and sap from infected Edgecote Purple was always used as the source.of the virus.

In the hybrid progenies the same range of symptoms was obtained with virus 'C' as with virus 'Y' and the same principle was adopted for the classification of hypersensitive and non-hypersensitive plants as was done in the case of virus 'Y'.

With virus 'C' also Cockerham obtained anomalous segregation ratios of hypersensitive to non-hypersensitive plants, that is, in the progeny G 614(a) raised from the cross Solanum simplicifolium X Solanum Rybinii, he obtained approximately 7:1 ratio of hypersensitive to non-hypersensitive plants.

Table 12 shows that the progeny G 1132(a), raised from the reciprocal cross gave approximately 1:1 ratio, which was also obtained in the progenies G 1131(a) and G 1131(c), both of which <u>was</u> raised from the were/ cross Solanum brevimucronatum X Solanum simplicifolium.

The same explanation can also be put forward to explain the reason for the excess of hypersensitive plants in the progeny tested by Cockerham, that is, the excess is due to high degree of female sterility present in Solanum simplicifolium.

Hence in this case also the 1:1 ratio obtained in the F_1 progenies is confirmed.

To avoid further anomalies, the same care

Table--12.

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			N C	n c	N C	n c	χ^2	D.F.	P	
G1132(a)	S.Rybinii x S.simplicifolium	96	45	51	48	48	·26	1	0.7-0.5	n n x N n c c C c
G1131(a)	S.brevimucronatum x S.simplicifolium	74	40	34	37	37	·42	1	0.7 -0.5	Do.
G1131(c)	Do.	30	18	12	15	15	·6	1	0.5-0.3	Do.

Table--13.

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			$\frac{N}{C}$	$\frac{n}{c}$	$\frac{N}{C}$	$\frac{n}{c}$	χ^2	D.F	P	
G1201	G614(a)21 x G614(a)7	50	34	16	37·5	12·5	1·3	1	0·3-0·2	$\frac{N}{C}\frac{n}{c} \times \frac{N}{C}\frac{n}{c}$
G1239	G614(a)5 x G614(a)25	49	25	24	24·5	24·5	·02	1	0·9-0·8	$\frac{N}{C}\frac{n}{c} \times \frac{N}{C}\frac{n}{c}$
G1275	G1132(a)13 x G614(a)16	61	28	33	30·5	30·5	·408	1	0·7-0·5	Do.

was taken, as it was done in the cases of viruses 'A' and 'Y' by selecting all the material used in the present studies with due regard to the presence of female sterility in the progenies derived from Solanum simplicifolium.

Table 13 shows that the progeny G 1201, which was raised by intercrossing two hypersensitive plants, selected from the F_1 progenies, segregated approximately in the ratio, 3:1. Other two progenies G 1239 and G 1275, which were raised by crossing the hypersensitive plants selected from the F_1 progenies with the non-hypersensitive plants, gave approximately 1:1 ratio of hypersensitive to non-hypersensitive plants. From these results it can be concluded that in these plants, hypersensitive reaction to virus 'C' is controlled by a single dominant gene.

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Linkage between the genes N_Y, N_C and N_A.

It has already been shown in the previous chapters that in the progeny G 614(a), which was raised from the cross Solanum simplicifolium X Solanum Rybinii, Cockerham found that the plants hypersensitive to the three viruses 'Y', 'C' and 'A' were identical. This result called for further investigation to examine the possibilities that, either a single genetic unit controlled reactions to the viruses 'Y', 'C' and 'A' or that the three genes were very closely linked.

The first step was taken for this investigation by examining the progeny G 1132(a) which was derived from the reciprocal cross, Solanum Rybinii X Solanum simplicifolium.

Each of the plants of this progeny was tested with viruses 'Y', 'C' and 'A' and Table 14 shows that the data obtained from this progeny does not follow the pattern of the anomalous progenies tested by Cockerham. On the contrary plants with different gene combinations have been obtained, suggesting that the hypersensitive reaction to the three viruses are controlled by three different genes. The same result was obtained from two other progenies, G 1131(a) and G 1131(c), raised from the cross Solanum brevimucronatum X Solanum simplicifolium. Moreover it has already been established in the previous chapters that the hypersensitive reaction to each of the three viruses, "Y", "C" and "A" is conditioned by a single dominant gene.

Hence, from these results, the possibility of a single gene being responsible for the hypersensitive reactions to all the three viruses can be eliminated and Cockerham's data can be explained by the fact that the segregation in the progeny G614(a) is anomalous, due to the reasons as described in the previous chapters.

In the following work the second possibility, that the genes are linked, has been investigated.

It has already been shown that Solanum simplicifolium is heterozygous for three dominant genes, N_Y, N_C, and N_A; each controlling hypersensitive reaction to the viruses "Y", "C" and "A" respectively. Hence the information on the linkage between the genes in the coupling phase can be obtained by crossing Solanum simplicifolium with plants, recessive for all the three genes.

The material for this study was raised from the crosses Solanum Rybinii x Solanum simplicifolium and Solanum brevimucronatum x Solanum simplicifolium, where Solanum Rybinii and Solanum brevimucronatum were used as recessive plants, because of their non-hypersensitive nature. The data from the progeny G614(a), as obtained by Cockerham has not been taken into consideration because of its anomaly in the segregation and in all the above mentioned crosses Solanum simplicifolium has been used as a pollen parent, to avoid any anomaly due to the female sterility existing in Solanum simplicifolium.

Each plant of the progenies raised from the crosses Solanum Rybinii x Solanum simplicifolium and Solanum brevimucronatum x Solanum simplicifolium has been tested with the three viruses. These progenies, of course, have already been tested for their single factor segregation.

Table-I4.

Gene Combinations	Frequencies of Combinations			Total
	GII32(a)	GII3I(a)	GII3I(c)	
YCA	20	25	I4	59
yca	I9	2I	I0	50
Yca	4	7	I	I2
yCA	2	5	0	7
YCa	0	0	0	0
ycA	0	2	0	2
YcA	0	I	I	2
yCa	I	3	4	8
Total	46	64	30	I40

Detection of Linkage:---

As all the progenies tested have been raised by crossing Solanum simplicifolium, heterozygous for the three genes, with plants recessive for all the three genes, plants of eight different gene combinations are expected in the progenies. Table 14 shows the expected different gene combinations and the observed frequencies of the combinations in the three progenies.

For the detection of linkage, the data from these progenies have been analysed by χ^2 method (Mather. 1938; text) and (Fisher 1941 text):- the theoretical extectation being that, since all the three progenies are derived from triple hetrezygotes crossed with triple recessives, the eight classes should appear in equal numbers, corresponding to the hypothesis that in each factor the allelomorphs occur with equal frequency and that the three factors are independent in their segregations.

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χ^2 is partitioned into six components , three of which are concerned with the deviation of the single genes from the expected ratios and the other three are involved in an enquiry into the linkage of the three pair of genes; the expectation being that the genes concerned are independent in their segregations. In table 15 the values of the components of χ^2 for one degree of freedom in each case has been shown for each of the three individual progenies and table I6 gives the values of the components of χ^2 calculated on the totals of the progenies. It can be seen in table I5 that none of the χ^2s concerned with deviation of the single factors are significant but the components of χ^2 for the linkage between each of the pair of factors for one degree of freedom is highly significant in each of the three progenies. Table I6 shows that the χ^2 for the deviation of the single factors, calculated on the totals of the progenies are also not significant at all; on the other hand each of the three χ^2s for the three pairs of gene association are highly significant, which suggests the linkage between the pairs of genes.

The heterogeneity for each of the components between the three progenies has been tested and it is shown in table I6, that in none of the cases it is significant. Hence the three progenies have been considered homogeneous and from the results it can be concluded that the three families agree significantly in showing that there is no agreement with the hypothesis of independent segregation of the genes concerned but the three genes are linked in the coupling phase.

Table--15

Progenies	Components of						
	Y,y	C,c	A,a	YC	CA	AY	D.F
G 1132(a)	0·087	0	0·087	22·260	42·086	25·130	1
G 1131(a)	0·062	0·062	0·062	16	42·250	20·250	1
G 1131(c)	0·133	1·20	0	10·800	13·333	26·133	1
Total	0·282	1·082	0·149	49·060	97·689	71·513	3

Table--16

Progenies	Total	Deviation			Heterogeneity	
	χ^2	D.F	P	χ^2	D.F	P
Y,y	0·257	1	0·7 - 0·5	0·025	2	0·99 - 0·98
C,c	0·457	1	0·5 - 0·3	0·525	2	0·8 - 0·7
A,a	0	1		0·149	2	0·95 - 0·9
Y C	48·028	1	less than ·001	1·032	2	0·72 - 0·5
C A	96	1	Do.	1·689	2	0·5 - 0·3
A Y	68·600	1	Do.	2·913	2	0·3 - 0·2

Estimation of Linkage:-

The linkage values between the three genes have been calculated in three different groups, the groups being differentiated on the three pairs of gene associations, as, N_YN_C, N_CN_A and N_AN_Y. It has already been shown that the data from the three progenies are homogeneous. Therefore, the data from the three progenies have been grouped in tables I7, I8 and I9 according to the three pairs of genes, for the estimation of linkage between the gene pairs N_YN_C, N_CN_A and N_AN_Y respectively.

As the linkage between the genes are in the coupling phase, the linkage values have been calculated by the frequency of recombinations or p; which has been calculated on the formula, $p = \frac{a2+a3}{n}$ (a_I, a2, a_3 & a_4 representing the frequencies of the four combinations, a_2 and a_3 being the recombinations and n being the total number of plants) (Mather I938 text).

Table I7 shows the linkage value between the genes N_y and N_c is 20·7I4 %.

The linkage value between the N_c and N_A, and N_A and N_Y has also been calculated on the same principle and tables I8 and I9 show that the linkage values between the genes N_C and N_A is 8·57I % and that between the genes N_A and N_Y is I5.

Hence from these results the following

Table--17

Progenies	Frequencies of Combinations				Total	Linkage Value in per cent	Standard Error
	YC	Yc	yC	yc			
G1132(a)	20	4	3	19	46	15·217%	± 5·3%
G1131(a)	25	8	8	23	64	25%	± 5·4%
G1131(c)	14	2	4	10	30	20%	± 7·1%
Total	59	14	15	52	140	20·714%	± 3·3%

∴ Linkage value between N_Y and N_C = 20·714%

Table--18

Progenies	Frequencies of Combinations				Total	Linkage Value in per cent	Standard Error
	CA	Ca	cA	ca			
G1132(a)	22	1	0	23	46	2·173%	± 0·7%
G1131(a)	30	3	3	28	64	9·375%	± 3·6%
G1131(c)	14	4	1	11	30	16·375%	± 6·7%
Total	66	8	4	62	140	8·571%	± 0·2%

∴ Linkage value between N_C and N_A = 8·571%

Table-- 19

Progenies	Frequencies of Combinations				Total	Linkage Value in per cent	Standard Error.
	AY	Ay	aY	ay			
G1132(a)	20	2	4	20	46	13·043 %	$\pm 4{\cdot}9$ %
G1131(a)	26	7	7	24	64	21·875 %	$\pm$ 5·1 %
G1131(c)	15	0	1	14	30	3·333 %	$\pm$ 3·2 %
Total	61	9	12	58	140	15 %	$\pm 0{\cdot}3$ %

$\therefore$ Linkage value between N_A and N_Y = 15·00 %

conclusions can be drawn.

(1) that the three progenies are homogeneous,

(2) that in each family there is no agreement with the hypothesis of independent segregations of the genes.

(3) that the genes N_Y, N_C and N_A are linked on the coupling phase and

(4) that the genes are arranged in the chromosome in the following order

N_Y------15-------N_A---8·571--N_C

------------20·714--------------

As the three genes are linked together, the frequency of double crossovers ie. of the plants with the gene combinations Yy Cc aa and yy cc Aa should be very small. Table 14 shows that the number of double cross-overs is 2 out of 140 plants ie. 1·4%, which seems to be quite compatible with the expectation.

EXPLANATION OF PLATE.1.

Fig.1:- Solanum simplicifolium grown in the field.

Fig.2:- Solanum Rybinii grown in the field.

Fig.3. Necrotic local lesions on inoculated leaves with virus "Y". of ?

Fig.4. Mottle symptom due to virus "Y" infection. on ?

------- x -------

PLATE . 1

Fig. 1.

Fig. 2.

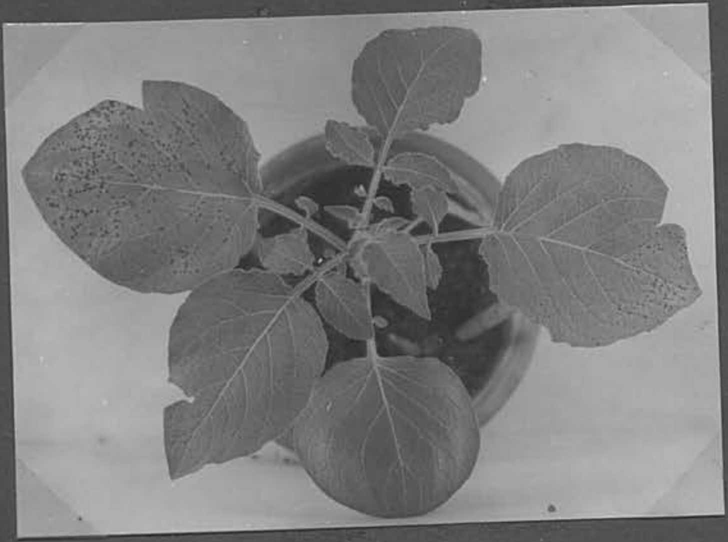


Fig. 3.

Fig. 4.

EXPLANATION OF PLATE. 2.

Fig. 1.:- Single leaves showing necrotic local lesions with virus "Y".

of ?

(a) upper surface; (b) Under surface.

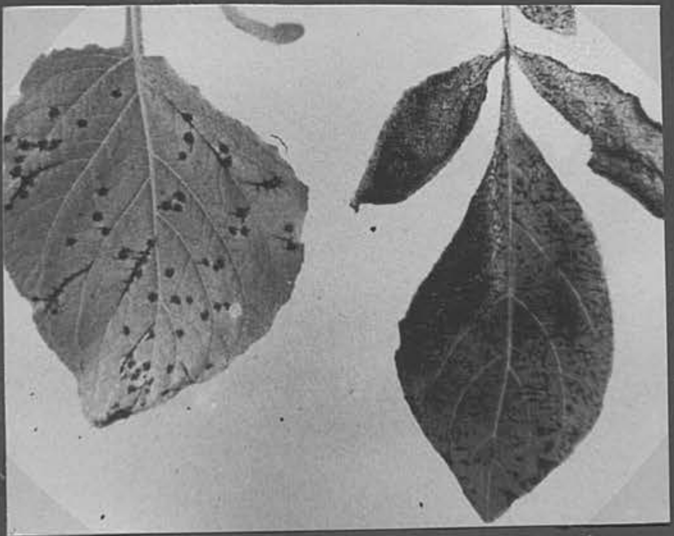
Fig.2.:- Comparison between necrotic lesions from infection by sap-inoculation and by grafting.

what ?

(a) Sap-inoculation; (b) Grafting.

PLATE. 2.

(a.) Fig. 1 (b)



(a) Fig. 2. (b)

EXPLANATION of PLATE. 3.

Fig. 1.;- Seedling, showing top necrotic reaction with virus "Y" by sap-inoculation. of ?

Fig.2.:- Early stage of systemic lethal necrosis in ? with virus "Y". by graft-infection.

Fig.3.:- Early and final stage of systemic lethal necrosis, from infection with virus "Y" by grafting. in ?

(a) Early stage. (b) Final stage.

------- x -------

PLATE. 3.

Fig. 1.

Fig. 2

(a) Fig. 3 (b)

EXPLANATION OF PLATE.4.

Fig.1:- Seedling showing necrotic local lesions on inoculated leaves with virus "C". of?

Fig.2:- Top-necrotic type of symptom. Seedling infected with virus "C" by sap-inoculation. of?

Fig.3:- Early stage of systemic lethal necrosis on seedling infected with virus "C" by sap-inoculation. of?

------- x -------

PLATE. 4.

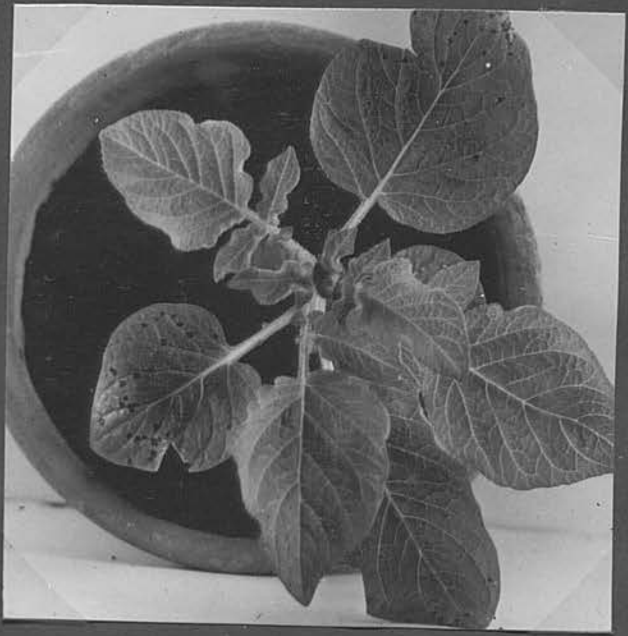


Fig. 1.

Fig. 2.

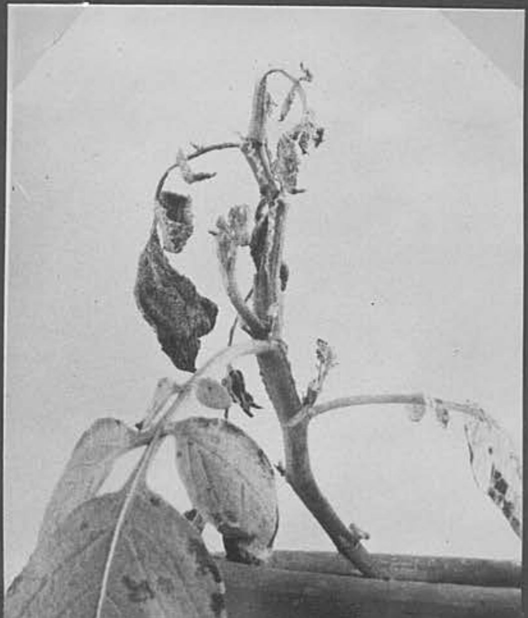


Fig. 3.

EXPLANATION. OF PLATE.5.

Fig.1:- Systemic lethal necrosis on seedling infected with virus "A" by grafting. of ?

Fig.2:- Mottle symptom due to virus "A" infection. in ?

------- x -------

PLATE. 5.

Fig. 1

Fig. 2.

EXPLANATION OF PLATE.6.

Fig. 1:- Seedling showing necrotic local lesions on inoculated leaves with virus"X". < of ?

Fig.2:- Early stage of systemic lethal necrosis with virus "X" (infection by sap-inoculation.) in ?

Fig.3:- Later stage of systemic lethal necrosis shown by plant grown from necrotic tubers obtained from plants showing hypersensitive reaction in the previous year. of ?

------- x -------

Fig 4 ?

PLATE. 6.

Fig. 1

Fig. 2

Fig. 3.

Fig. 4.

SECTION. 11.

INHERITANCE OF COLOUR FACTORS.

Review of Literature.

A wide range of colour exists in the potato, but primarily the colour can be classified into two main groups, reddish purple and bluish purple. Both groups of colour occur in a wide range of shades and intensities, ranging from a very faint pale colour to deep bright colour. In addition there is a wide range of distribution of colour ranging from just a slight trace in certain parts to self coloured plants. Moreover the intensity of colour also varies with exposure to light, some tubers showing no colour in absence of light but an appreciable amount of colour on exposure to light. The intensity of pigmentation is also increased with prolonged exposure.

plants or tubers ?

In the past, several workers have studied the inheritance of colour in the potato and various factorial hypothesis have been suggested. Most of the work has been done with the cultivated varieties of potatoes.

Salaman (1910, 1926) showed that blue colour is dominant over red, both being dominant over white. The following factor hypothesis has been suggested by Salaman to explain the inheritance of tuber colour in the potato: R, a red colour producing factor which in presence of the basic factor D converts the chromogen into red pigments and the factor P which is responsible for the blue colour. The factor P can act only in presence of the factors R and D. The degree of redness is dependent on the homogeneous condition or otherwise of the plants with regards to the factors R and D. Salaman also suggested two other factors E and S responsible for the distribution of colour on the tubers; E being responsible for coloured eyes and S for the distribution of colour on the surface of tubers.

Stuart (1915) disagreed with Salaman's hypothesis, that white colour is a recessive character, because in some of his crosses there was a predominance of white tubered seedlings. But this view is more or less contrary to general opinion.

Müller (1923) has explained his results with the help of the complementary factors G and H and an inhibitory factor Y, which inhibits the action of G and H. He also reported some of the crosses where white colour seemed to be dominant. He found three factors B, D and E, necessary for the appearance of colour in the stems. These three factors are complementary to each other. Besides these factors, he also reported the presence of an inhibitory factor, H, in some of his seedlings. According to him a single factor A conditions the flower colour in potatoes.

Kelly (1924) explained the results from

selfing and crossing the parti-coloured variety McCormick, with the help of a basic factor B, a diluting factor D and a restricting factor M.

But Krantz (1925) failed to confirm Kelly's conclusion and found the following factors responsible for the inheritance of tuber colour. He found the factors R and A producing red colour, and a basic factor D for making the pigment. D and R alone with A gives only a parti-coloured tuber, while A added to them gives an even distrubution of the colour pigment over the whole surface of the tubers. In later papers, Krantz (1926, 1932) reported the following factors and their relationship to tuber colour. For producing tuber colour type with colour in the cork layer, he described the factors D, S, E, A and P; where D and S acts as basic factors. For the other tuber colour type with colourless cork layer he described the factors C, R, T and B, where the first three are complementary factors which must all be present in order to produce red colour. B changes the red colour to blue colour. Krantz and Mattson (1936) and Krantz (1936) studied the segregation of the periderm coloured progenies and found that the complementary actions of the factors E, S and F produced red colour in the periderm and that certain parents carried duplicate factors. The inheritance of cortex colour has been explained by assuming the complementary actions of the factors C, R and D, blue colour in periderm and cortex has been suggested to be due to two factors P and P; each capable of changing red colour into blue. The observation suggested that while certain factors effects colour only in one tissue other factors influence in both periderm and cortex.

Köhler (I927) concluded that the inheritance of colour in potatoes can be explained with the help of Salaman's hypothesis.

Asseyeva (I928) distinguished the factor R, closely related to the factor described by Salaman. Besides the factors D, R, R_I and P he also described another factor A, which was responsible for the colouration of the eye, which is active only in presence of the factor D. The plants with the combination Da will have white tubers with pink eyes while the plants with the combinations DRA and PDRA produces red and purple coloured tubers respectively. both with dark eyes and in absence of A the tubers will have light coloured or colourless eyes. In a later paper Asseyeva and Necoleava (I935) reported that the factors R and D are common for the manifestation colour in all organs. They distinguished another set of factors D, E, M, F and S, they described as factors for development of colour and which determine the distribution of pigments and differ accordingly to the regions of their activity. The factors D, E and M are responsible for the development of colour in the tubers, while F and S acts in the flower. They also reported the presence of a duplicate set of factors P,R,D,^{E} and F, entirely similar to the main ones. In the sprout colour all the above mentioned factors take part with the exception of the factor F. In the presence of F alone or when completely recessive the sprouts are either totally colourless or have only a feeble purple pink colouration.

Sirks (I929) reported that for the development of red and blue colour over the whole surface of the tubers it is necessary that both the basic factors D and S be present with R or P or both, which are responsible of red or blue colour respectively; P being epistatic to R, The colouring of the eyes being dependent on one or boththe factors P and R, together with S. He disagreed with Salaman who stated that both D and R are necessary for the expression of P. The red and the blue colour in the internodes are also conditioned by the factors R and P respectively, but in the older internodes the colour depends on R and P together with the factor D and both R and P are kryptomeric in absence of D.

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Clark and Stevenson (I935) showed that their results were in accordance with Salaman's hypothesis, that the action of complementary factors, designated as D and R are necessary for producing red colour and in addition of a third factor P producing blue colour.

Lunden (I929, I932) described a basic

factor B, which alone produces faint reddish tuber colour the factor~~s~~ P as blue colour producing factor and the factor A as intensifying factor to the factor B. Later after making an extensive study on the inheritance of colour in potato, he (1937) described the following factors for the manifestation of colour. He described factor R as a factor for red coloured tuber with colour only in the cortex and another factor E which also produces red coloured tuber with colour chiefly in the periderm. Another factor D which he stated to be complementary to both R and E. Both R ~~and~~ E and D all produce ~~acts~~ for the colour in the sprout, stem internodes, petioles and inflorescence . The factor D in absence of R and E gives some anthocyamin colour in the stem and inflorescence as well as red purple sprout with coloured tips. The factor P controls the blue purple colour and in its presence the red purple colour is converted into blue purple colour and both P+R and P+E gives respectively, in absence of D, pale blue coloured tubers of both colour types. He described the factor F for flower colour, which is complementary to the factor D, and ~~flowers~~ in absence of D and G which is another complementary factor of F besides D, F produces red purple colour flowers. Lunden also described the following factors over and above those above-mentioned factors; the factor S, responsible for distribution of colour on the surface of tubers; the factors

W and V which acts for the normal chlorophyll formation.

All the above mentioned works have been done with the cultivated varieties of potatoes. Emme (1936, 1937) has published some on the inheritance of colour in 24-chromosome potatoes. She reported that the genetic factors concerned with the production of various colours on the petals of the flowers can be postulated as follows:--

An^{sp} :- the factor controlling the presence of colour on the upper surface of the corolla,

An^{inf} :- the corresponding factor for the presence of colour on the under surface of the corolla.

She also designated two other factors C_r and C_y which are responsible for reducing and raising the pH in the cells of the corolla, resulting in the production of shades ranging from reddish purple to raspberry red in the first case and in the second case producing a blue purple or blue shade. The loci C_r and C_y are considered to be the sites of a series allelomorphs conditioning an infinite variety of colours due to these two genes. She also reported that blue colour is dominant to red and that both blue and red are dominant to white. The genotypic constitutions of Solanum Rybinii, and Solanum goniocalyx and Solanum stenotomum have been suggested to be An^{sp} an^{sp} Cr cr, $an^{sp}an^{sp}$ Crcr and

An^{sp} An^{sp}crcr respectively.

Chouduri (I942) reported that in the flowers of the progenies raised from the cross between Solanum Rybinii and Solanum demissum, there are two factors, R^I and R^2 for red colour. Blue colour is conditioned by the factor B, which is epistatic to both R^I and R^2. R^I alone produces red colour on the under surface of the petals and has ant cumulative effect with R^2; and R^I produce blue purple colour in combination with B. Where as R^2 alone produces more intense colour over a larger area and in combination with B produces a deeper blue purple colour.

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Materials and Methods.

Most of the material used in this investigation was obtained from the material raised for the investigation of inheritance of hypersensitive reaction. The progenies tested were derived from Solanum simplicifolium (C.P.C. 51A), Solanum Rybinii (C.P.C. 1311) and Solanum Rybinii (C.P.C. 979). Tubers of both Solanum simplicifolium and Solanum Rybinii (C.P.C. 1311) are white in absence of ~~light~~ exposure to light, but tubers of the first species show light bluish purple colour and of the second show faintly reddish purple colour on exposure to light. Solanum simplicifolium has completely white flowers and Solanum Rybinii (C.P.C. 1311) has white flowers with a very faint tinge of reddish purple colour on the under surface of the petals. Solanum Rybinii (C.P.C. 979) has deep bluish purple coloured tubers, stems and flowers.

The method of classifying colour is described in the experimental results.

Tubers were examined for colour shortly after harvest and again after exposing them to diffused light for 2 to 3 days. Flower colours were recorded as the plants started flowering. Seedlings for colour observations were raised from seed sown in sand contained in paper boxes or on fi~~t~~ter papers soaked with water in Copenhagen tanks. l/

To record the colour of the seedlings before exposure to light, all the seedlings were grown in the dark till they were nearly one inch tall. Then all the coloured seedlings were removed and counted, and the remaining colourless seedlings were exposed to light for about ten days. Where possible the distribution of reds and blues in the seedlings showing colour was recorded.

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Experimental Results.

It has already been reported that a wide range of bluish purple and reddish purple colours exists in potatoes. For convenience these two colours are referred to as blue and red throughout this paper and intensities have been classified into two groups, "deep" and "flush".

Table 1 shows the segregation of blue, red and white tubers and table 2 shows the segregation of coloured and white tubers in the progenies tested. As many tubers showed no colour in the absence of light, but produced an appreciable amount of pigment on exposure to light, all colours recorded in these two tables were obtained after exposing the tubers to light for 2 to 3 days.

All the tubers in progenies G 614(a) and G1132(a) raised from direct and reciprocal crosses between Solanum simplicifolium and Solanum Rybinii were blue. As Solanum simplicifolium and Solanum Rybinii have blue and red colour respectively, it shows that blue colour is completely dominant to red.

Some plants with blue tuber colour from the progeny G 614(a) were intercrossed and table 2 shows that the progeny G 950 gave a ratio of 7 coloured: 1 white, and the two reciprocal progenies G 1035(a) and G 1047(a) gave a ratio of 3 coloured : 1 white. Table 1 shows that in those two sets of progenies

Table--1

Segregation of tuber colour (Blue : Red : White)

Progenies	Parentage	Total	Observed			Expected			Deviation			Suggested Genotype
			Blue	Red	White	Blue	Red	White	χ^2	D.F	P	
G614(a)	S.simplicifolium x S.Rybinii	29	29	0	0	29	0	0	0	1		BBrr x bbRr
G1132(a)	S.Rybinii x S.simplicifolium	50	50	0	0	50	0	0	0	1		bbRr x BBrr
G 950	G 614(a) 7 x G 614(a) 10	45	32	7	6	33.75	5.62	5.62	0.122	1	0.8-0.7	Bbrr x BbRr
G1035(a)	G614(a)7 x G614(a)8	70	53	0	17	52.5	0	17.5	0.018	1	0.9-0.8	Bbrr x Bbrr
G1o47(a)	G614(a)8 x G614(a)7	29	22	0	7	21.75	0	7.25	0.01	1	0.95-0.9	Bbrr x Bbrr
G 941(b)	G614(a)15x CPC 979	12	11	0	1	9	2.25	0.75	0.76	1	0.5-0.3	BbRr x BbRr
G 937(a)	G614(a)7 x CPC 979	89	62	13	14	66.75	11.12	11.12	1.34	1	0.3-0.2	Bbrr x BbRr

Table--2.

Segregation of tuber colour (Coloured : white) :-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G614(a)	S.simplicifolium x S.Rybinii	29	29	0	29	0	0	1		BBrr x bbRr
G1132(a)	S.Rybinii x S.simplicifolium	50	50	0	50	0	0	1		bbRr x BBrr
G 950	G614(a)7 x G614(a)10	45	39	6	39.38	5.62	0.027	1	0.9-0.8	Bbrr x BbRr
G1035(a)	" 7 x " 8	70	53	17	52.5	17.5	0.018	1	0.9-0.8	Bbrr x Bbrr
G1047(a)	" 8 x " 7	29	22	7	21.75	7.25	0.01	1	0.95-0.9	Bbrr x Bbrr
G 941(b)	" 15 x "CPC979	12	11	1	11.25	0.75	0.138	1	0.9-0.8	BbRr x BbRr
G 937(a)	" 7 x "	89	75	14	77.87	11.2	0.8	1	0.5-0.3	Bbrr x BbRr

ratios of 6 blue : 1 red : 1 white and 3 blue : 0 red : 1 white respectively were obtained. Two other plants from the progeny G 614(a) were also crossed with a blue tubered variety of Solanum Rybinii (C.P.C 979) and tables 1 and 2 show that the progeny G 941(b) gave a ratio of 12 Blue : 3 red : 1 white, ie, 15 coloured : 1 white and the progeny G 937(a) gave a ratio of 6 blue : 1 red : 1 white ie, 7 coloured : 1 white. For convenience Solanum Rybinii (C.P.C 979) has been always mentioned as C.P.C 979.

The above mentioned results show that the ratios of 15 coloured : 1 white, 7 coloured : 1 white and 3 coloured : 1 white were obtained, which also agrees in the distribution of blues, reds and whites in them. These results suggest that blue and red colours in those plants are controlled by two factors B and R respectively.

More detailed results were obtained in the investigation of the inheritance of seedling stem colour in the progenies raised by intercrossing the plants selected from the progeny G 614(a). It will be seen in table 7 that the progeny G 1132(a), Solanum Rybinii x Solanum simplicifolium failed to segregate, all the seedlings having blue colour.

Segregations in the progenies raised by intercrossing plants from G 614(a) have been divided into three different groups according to the ratios obtained.

Table--3

Segregation of Seedling stem colour after exposure (15 coloured : 1 white):--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G 1209	G614(a)11 x G614(a)10	50	48	2	46.87	3.12	0.407	1	0.7-0.5	BbRr x BbRr
G1212	" 15 x " 10	15	15	0	14.07	0.93	0.99	1	0.5-0.3	Do.
G1215	" 21 x " 10	42	38	4	39.4	2.6	0.8	1	0.5-0.3	Do.
G1217	" 24 x " 10	40	36	4	37.5	2.5	0.96	1	0.5-0.3	Do.
G1219	" 33 x " 10	57	52	5	53.44	3.56	0.61	1	0.5-0.3	Do.

Table--4

Segregation of seedling stem colour after exposure (7 coloured : 1 white)

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	P	D.F	
G 1193	G614(a)5 x G614(a)7	68	61	7	59.5	8.5	0.29	0.7 -0.5	1	BbRr x Bbrr
G 1195	" 11x " 7	41	37	4	35.87	5.13	0.23	0.7 - 0.5	1	BbRr x Bbrr
G 1199	" 19x " 7	56	46	10	49	7	1.466	0.3 - 0.2	1	Do.
G1422	" 4 x " 10	31	28	3	27.15	3.85	0.2	0.7 - 0.5	1	Bbrr x BbRr
G 1210	" 13x " 10	33	29	4	28.27	4.13	0.001	0.98-0.95	1	Bbrr x BbRr
G 1211	" 14x " 10	49	44	5	42.47	6.12	0.22	0.7 - 0.5	1	Bbrr x BbRr
G 1214	" 17x " 10	12	10	2	10.5	1.5	0.18	0.7 - 0.5	1	Bbrr x BbRr
G 1220	" 3 x " 16	87	77	10	76.15	10.85	0.07	0.8 - 0.7	1	BbRr x Bbrr
G 1222	" 5 x " 16	60	53	7	52.5	7.5	0.03	0.9 - 0-8	1	BbRr x Bbrr
G 1225	" 11x " 16	72	65	7	63	9	0.50	0.5 - 0.3	1	BbRr x Bbrr
G1227	" 15x " 16	46	39	7	40.25	5.75	0.30	0.7 - 0.5	1	BbRr x Bbrr
G 1229	" 19x " 16	36	29	7	31.5	4.5	1.57	0.3 - 0.2	1	BbRr x Bbrr
G 1233	" 29x " 16	36	29	7	31.5	4.5	1.57	0.3 - 0.2	1	BbRr x Bbrr
G 1235	" 33x " 16	52	41	11	45.5	6.5	3.55	0.1 - 0.05	1	Do.
G 1237	" 3 x " 25	49	40	9	42.9	6.1	1.56	0.3 - 0.2	1	Do.

Table--5

Segregation of seedling stem colour after exposure (3 coloured : 1 white):--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G 1221	G614(a)4x G614(a)16	61	45	16	45.75	15.25	0.04	1	0.9-0.8	Bbrr x Bbrr
G 965	" 7 x " 16	30	24	6	22.5	7.5	0.4	1	0.7-0.5	Do.
G 1063	" 8 x " 16	86	62	24	64.5	21.5	0.38	1	0.7-0.5	Do.
G 1226	" 14 x " 16	76	60	16	57	19	0.62	1	0.5-0.3	Do.
G 1064	" 25 x " 16	24	18	6	18	6	0	1		Do.

Thus in tables 3, 4 and 5 there are collected progenies segregating in the ratios 15:1, 7:1 and 3:1 respectively.

It was very difficult in all the progenies to record the distribution of blue and red. In table 6 however, the segregations of blue, red and white, in some of the progenies examined are given. It can be seen from this table that the first three progenies, which segregated in the ratio 15:1 for coloured : white gave a ratio of 12 blue : 3 red : 1 white, and that two other progenies which segregated in the ratio 7 : 1 for coloured : white gave 6 blue : 1 red : 1 white. These results are in agreement with the results obtained from the tubers.

The 15 : 1 ratio obtained in the first group of plants suggests that, there are two factors segregating for colour in those groups of plants. On comparing these results with the results obtained for the segregation of blues, reds and whites in table 6, it can be concluded that a single factor is responsible for red colour which can be designated as R and another factor which can be designated as B, controls the blue colour and is dominant to the factor R. This conclusion also holds good for the other two groups of progenies segregating in 7:1 and 3:1 ratio for coloured : white.

These progenies segregating in the ratio 15:1 for colour: white may be assumed to have been raised by intercrossing plants of genotypes BbRr. Similarly progenies segregating in the ratios 7:1 may be assumed

Table--6

Segregation of seedling stem colour after exposure (Blue : Red : White):--

Progenies	Parentage	Total	Observed			Expected			Deviation			Suggested
			Blue	Red	White	Blue	Red	White	χ^2	D.F	P	Genotype
G1219	G614(a)33 x G614(a)10	57	39	13	5	42.74	10.68	3.5	1.41	1	0.3-0.2	Bbrr x Bbrr
G1215	" 21 x " 10	42	28	10	4	31.5	8	2.5	1.48	1	0.3-0.2	Do
G1212	" 15 x " 10	15	12	3	0	11.25	2.81	0.93	0.93	1	0.5-0.3	Do
G1195	" 11 x " 7	41	29	8	4	30.75	5.12	5.12	1.6	1	0.3-0.2	Do
G1214	" 17 x " 10	12	8	2	2	9	1.5	1.5	0.43	1	0.7-0.5	Do

Table--7

Segregation of seedling stem colour after exposure (coloured : white):--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F.	P	
G1132(a)	S.Rybinii x S.simplicifolium	31	31	0	31	0	0	1		bbRr x BBrr
G1067	S.Rybinii x G 614(a) 16	48	33	15	36	12	1	1	0.5 - 0.3	bbRr x Bbrr
G1086	S.Rybinii x G 614(a) 31	47	33	14	35.25	11.75	0.57	1	0.5 - 0.3	bbRr x Bbrr
G1167	G 614(a) 8 x S.Rybinii	82	66	16	61.5	20.5	1.3	1	0.3 - 0.2	Bbrr x bbRr
G1170	G 614(a) 23 x S.Rybinii	72	57	15	54	18	0.66	1	0.5 - 0.3	Bbrr x bbRr
G1171	G.614(a) 25 x S.Rybinii	92	74	18	69	23	2.22	1	0.2 - 0.1	Bbrr x bbRr

to have been raised from the cross BbRr x Bbrr or its resiprocal and the third group of progenies segregating in the ratio 3:1 to have been raised from the cross Bbrr x Bbrr.

Comparing these four tables (3, 4, 5 and 6) the factorial constitutions of the parents involved in raising these progenies are obtained as shown in table 8.

Table 8.

Ref. No.		Suggested genotype	Ref.No.	Suggested genotype
G 614(a)	3	Bb Rr	G614(a) 16	Bb rr
"	4	Bb rr	17	Bb rr
"	5	Bb Rr	19	Bb Rr
"	7	Bb rr	21	Bb Rr
"	8	Bb rr	23	Bb rr
"	10	Bb Rr	24	Bb Rr
"	11	Bb Rr	25	Bb rr
"	13	Bb rr	29	Bb Rr
"	14	Bb rr	31	Bb rr
"	15	Bb Rr	33	Bb Rr

All these parents were the plants from the progeny G 614(a) which was derived from the cross Solanum simplicifolium x Solanum Rybinii.

Now, table 8 shows that out of 20 plants belonging to the progeny G 614(a), 10 were of the constitution Bb Rr and 10 of Bb rr. Moreover, by crossing Solanum simplicifolium and Solanum Rybinii all the tubers and seedling stems obtained were blue. Hence it would seem that Solanum simplicifolium is homozygous for B.

From these results, it can be concluded that the factorial constitution of Solanum simplicifolium is BB rr and that of Solanum Rybinii is bb Rr. Table 7 gives the segregation of the progenies raised by crossing Solanum Rybinii with some of the plants from the progrny G 614(a). It shows that the data obtained in table 7 also is in agreement with the hypothesis that Solanum are / Rybinii is of the constitution bb Rr. Similarly it can also be shown that the factorial constitution of Solanum Rybinii (C.P.C. 979) is Bb Rr.

Many of the plants in the progenies tested showed no colour in absence of light, but on exposure to light they produced an appreciable amount of pigment. It has been shown in table 7 that all the seedlings raised from the cross between Solanum simplicifolium and Solanum Rybinii had blue colour on their stem. Before exposure to light, however, none of these seedlings showed any colour. (Table 9)

A number of progenies were examined for seedling stem colour both before and after exposing them to light. After being exposed to light these progenies gave segregation ratios of 15:1, 7:1 or 3:1 and they are

Table--9

Segregation of seedling colour before exposure (coloured : white):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G1132(a)	S.Rybinii x S.simplicifolium	31	0	31	0	31	0	1		BbRrHh x BBrrHH
G1086	S.Rybinii x G 614(a) 31	47	0	47	0	47	0	1		BbRrHh x BbrrHH
G1167	G 614(a) 8 x S.Rybinii	82	0	82	0	82	0	1		BbrrHH x BbRrHh
G1170	G 614(a) 23 x S.Rybinii	72	0	72	0	72	0	1		BbrrHH x BbRrHh
G1171	G 614(a) 25 x S.Rybinii	92	0	92	0	92	0	1		BbrrHH x BbRrHh

Table--10

Segregation of seedling stem colour before exposure (coloured : white) :--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G1209	G614(a)11 x G614(a)10	50	22	28	16.4	33.59	2.84	1	0.1-0.05	BbRrHh x BbRrHh
G1217	G614(a)24 x " 10	40	6	34	8.75	31.25	1.1	1	0.3-0.2	BbRrHH x BbRrHh

Table--11

Segregation of seedling stem colour before exposure (coloured : white):--

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G1211	G614(a)14 x G614(a)10	49	19	30	16.84	32.16	0.41	1	0.7-0.5	BbrrHh x BbRrHh
G1220	" 3 x " 16	87	26	61	29.9	57.09	0.7	1	0.5-0.3	BbRrHh x BbrrHh
G1222	" 5 x " 16	60	23	37	20.62	39.37	0.38	1	0.7-0.5	BbRrHh x BbrrHh
G1225	" 11 x " 16	72	24	48	24.75	47.25	0.03	1	0.9-0.8	BbRrHh x BbrrHh
G1235	" 33 x " 16	52	14	38	17.87	34.12	1.12	1	0.3-0.2	BbRrHh x BbrrHh
G1422	" 4 x " 10	31	2	29	3.87	27.13	0.94	1	0.5-0.3	BbrrHH x BbRrHh

Table--12

Segregation of seedling stem colour before exposure (coloured: white):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	χ^2	D.F	P	
G 1221	G614(a)4 x G614(a)16	61	11	50	7·25	53·75	2·19	1	0·2-0·1	BbrrHH x BbrrHh
G 965	" 7 x " 16	30	6	24	3·75	26·25	1·6	1	0·2-0·1	Do.
G 1063	" 8 x " 16	86	5	81	10·75	75·25	3·45	1	0·1-0·05	Do.
G 1064	" 25 x " 16	24	2	22	3	21	0·37	1	0·7-0·5	Do.
G 1226	" 14 x " 16	76	22	54	23·75	52·25	0·17	1	0·7-0·5	BbrrHh x BbrrHh

included in tables 3, 4 and 5. The appearance of these progenies before exposure is given in tables 10, 11 and 12, the grouping again being according to the ratios in which they segregated after being exposed to light.

Thus the two progenies in table 10 segregated in the ratio 15 coloured : 1 white after exposure but as shown in this table, the segregations obtained before exposure were respectively 21 coloured : 43 white and 7 coloured : 25 white. Table 11 gives the segregation of the progenies segregating in the ratio 7 coloured : 1 white before exposure and it shows that the first five progenies gave a segregation approaching to the ratio 11 coloured : 21 white and the sixth one to a ratio of 1 coloured : 7 white before exposure to light. It has been shown in table 12 that 4 of the progenies which before exposure segregated in the ratio 3 coloured : 1 white gave a segregation of 1 coloured : 7 white and the fifth one segregated in the ratio of 5 coloured : 11 white. These results can be summed up in the following way:-

No. of progenies	Segregation ratio before exposure	Segregation ratio after exposure.
1	21 coloured:43 white	15 coloured:1white
1	7 coloured:25 white	
5	11 coloured:21 white	7 coloured:1white
1	1 coloured: 7 white	
4	1 coloured: 7 white	3 coloured:1white
1	5 coloured:11 white	

These data may be interpreted to indicate the presence of some factor which inhibits the development of pigment in these plants in absence of light. This inhibiting factor has been designated as H.

All the above mentioned results can be explained on the hypothesis that H is dominant to R or B or RB together, when one of them or both of them are heterozygous. Similarly HH is able to suppress colour expression with any combination of R or B or RB together. That is, one dose of H is required to inhibit the action of one dose of colour factor.

The ratios obtained in the progenies examined can be explained with the probable factorial hypothesis as given in the last columns of the tables 10, 11 and 12.

Now from tables 10, 11 and 12, it can be seen that five of the plants in the progeny G 614(a) are homozygous and 8 of them are heterozygous for the factor H, giving approximate ratio of 1HH:1Hh. This ratio can be obtained if one of the parents of G 614(a) is homozygous for H and the other is heterozygous. It has been already established that Solanum simplicifolium is homozygous for the factor B. Now, as Solanum simplicifolium does not show any colour in absence of light but rarely shows colour in the tuber with exposure, it seems evident that it is homozygous for H and Solanum Rybinii is heterozygous for H. Table 9 gives the segregation obtained in the progenies raised by crossing Solanum Rybinii with some of the plants from the progeny G 614(a), and it shows that the data obtained is quite compatible with the hypothesis.

Hence from these results it can be concluded that in the absence of light the factor H inhibits the effect of R or B or RB and one dose of H is necessary to inhibit one dose of colour producing factor. The factor H has no effect on the manifestation of colour in presence of light.

Both Solanum simplicifolium and all the coloured seedlings in the progenies raised from them had only light pigmentation, after being exposed to light; a condition which may be referred to as "flushed". No deep and self-coloured tubers or seedlings were found in this material. Solanum Rybinii (C.P.C 979) however, has deep self-coloured tubers and on crossing with some of the plants in progeny G 614(a) segregation for deep and flushed coloured tubers occurs in the approximate ratio 1:1. (Table-13)

This result calls for an additional intensifying factor D, which when present along with the colour producing factors R and B intensifies their effect and it seems evident that Solanum Rybinii (C.P.C 979) is heterozygous for the factor D and that both Solanum simplicifolium and Solanum Rybinii are recessive for this factor.

Table--13

Segregation of Tuber colour (Deep: Flush):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Deep	Flush	Deep	Flush	χ^2	D.F	P	
G 937(a)	G614(a)7 x C.P.C979	75	32	43	37·5	37·5	1·6	1	0·3-0·2	Bbrrdd x BbRrDd
G 941(b)	" 15 x "	11	6	5	5·5	5·5	0·092	1	0·8-0·7	BbRrdd x BbRrDd
G 955	C.P.C979 x G614(a)8	32	20	12	16	16	2	1	0·2-0·1	BbRrDd x Bbrrdd

Although it has been shown that all the tubers and seedlings of the progenies G 614(a) and G 1132(a) which were raised by crossing Solanum simplicifolium and Solanum Rybinii possessed factors for colour, the flowers produced by them had no colour on the upper surface of the petals. Solanum simplicifolium has completely white flowers and Solanum Rybinii has a very slight tint of red purple colour on the under surface of the petals. (Choudhuri 1942, thesis.).

In analysing the segregation of flower colour Emme (1936, 1937) has treated the colour of the two sides of petals separately and reported that two separate factors are responsible for the manifestation of colour on the upper and lower surface of the petals respectively. The following results on inheritance of flower colour are concerned with the manifestation of colour on the upper surface of the petals.

Tables 14 and 15 show that progenies raised from crosses between the white flowered Solanum simplicifolium. Solanum Rybinii and G 614(a) 23 failed to segregate all the flowers having white upper surfaces. On the other hand progenies raised by crossing white flowered Solanum Rybinii, G 614(a), G 614(a) 7, G 614(a) 8 and G 614(a) 13 with C. P. C 979, which has blue self-coloured flowers contained only plants with coloured flowers. Table 16 shows that the distribution of blue and red coloured flowers in all the progenies shown in table 15, is approximately of

Table--14

Segregation of flower colour (coloured: white):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	X^2	D.F	P.	
G 614(a)	S. simplicifolium x S. Rybinii	33	0	33	0	33	0	1		BBrrgg x bbRrgg
G1132(a)	S. Rybinii x S. simplicifolium	49	0	49	0	49	0	1		bbRrgg x BBrrgg
G1170(a)	G 614(a)23 x S. Rybinii	50	0	50	0	50	0	1		Bbrrgg x bbrrgg
G1178(a)	C.P.C 979 x S. Rybinii	46	46	0	46	0	0	1		BbRrGG x bbrrgg

Table--15

Segregation of flower colour (coloured: white):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Coloured	White	Coloured	White	X^2	D.F	P.	
G 937	G614(a)7 x C.P.C 979	48	48	0	48	0	0	1		Bbrrgg x BbRrGG
G 936	" 4 x "	11	11	0	11	0	0	1		Bbrrgg x BbRrGG
G 938	" 8 x "	10	10	0	10	0	0	1		Bbrrgg x BbRrGG
G 949	C.P.C979 x G614(a)7	14	14	0	12	0	0	1		BbRrGG x Bbrrgg
G 940	G614(a)13 x C.P.C979	8	8	0	8	0	0	1		Bbrrgg x BbRrGG

the ratio, 6 blue : 2 red.

These results in collaboration with the results obtained from the factorial analysis of the inheritance of colour in tubers and seedling stems of the parents concerned in tables 14, 15 and 16, indicate that, for the expression of colour on the upper surface of the petals, a distributing factor, which can be designated as G, is necessary. G itself in absence of any colour factor produces red colour and in presence of B and R produces blue and red colour respectively. On these assumptions it seems that C.P.C 979 is homozygous for the factor G and both Solanum simplicifolium and Solanum Rybinii are recessives for the factor.

The colour on the under surface of the flowers of Solanum Rybinii seems to be controlled by a different distributing factor, because in the progeny G1132(a) which was raised from the cross Solanum Rybinii x Solanum simplicifolium 24 plants had flowers with faint tint of colour on the under-surface of the petals and 26 plants had completely white flowers. This tends to show that the colour on the under-surface of flowers, as in Solanum Rybinii may be controlled by a separate distributing factor for which Solanum Rybinii ~~simplicifolium~~ seems to be heterozygous.

Attempts were also made to study the inter-relationship between the effects of the factors D and G in the flowers. According to the intensities of colour on the undersurface of the petals, the plants

Table--16

Segregation of flower colour (Blue: Red: White):-

Progenies	Parents	Total	Observed			Expected			Deviation			Suggested Genotype
			Blue	Red	White	Blue	Red	White	χ^2	D.F	P	
G 937	G614(a)7 x C.P.C979	48	32	16	0	36	12	0	1·77	1	0·2–0·1	Bbrrgg x BbRrGG
G 936	" 4 x "	11	8	3	0	8·25	2·75	0	0·029	1	0·9–0·8	Bbrrgg x BbRrGG
G 938	" 8 x "	10	7	3	0	7·5	2·5	0	0·13	1	0·8–0·7	Bbrrgg x BbRrGG
G 949	C.P.C979 x G614(a)7	14	11	3	0	10·5	3·5	0	0·09	1	0·8–0·7	BbRrGG x Bbrrgg
G 940	G614(a)13 x C.P.C979	8	6	2	0	6	2	0	0	1		Bbrrgg x BbRrGG

Table--17

Segregation of flower colour (Deep: Flush):-

Progenies	Parentage	Total	Observed		Expected		Deviation			Suggested Genotype
			Deep	Flush	Deep	Flush	χ^2	D.F	P	
G 937	G614(a)7 x C.P.C979	48	22	26	24	24	0·32	1	0·7–0·5	Bbrrddgg x BbRrDdGG
G 936	" 4 x "	11	5	6	5·5	5·5	0·08	1	0·8–0·7	Bbrrddgg x BbRrDdGG
G 938	" 8 x "	10	5	5	5	5	0	1		Do.
G 949	C.P.C979 x G614(a)7	12	5	7	6	6	0·32	1	0·7–0·5	BbRrDdGG x Bbrrddgg
G 940	G614(a)13 x C.P.C979	8	4	4	4	4	0	1		Bbrrddgg x BbRrDdGG

of the progenies, raised from some of the plants belonging to the progeny G 614(a) crossed with C.P.C 979, have been classified into two groups, as deep coloured and flushed coloured. The results of the segregations have been shown in table 16.

From these results it shows that D intensifies the factor G alone or in presence of R or B or RB together.

From the results obtained on analysis of the inheritance of colour in 24-chromosome potato plants examined, it shows that the same colour factors which produce colour in one part of the plant determine also the colour in all or several of the other parts of the plant. The followong pairs of factors have been found viz., Rr, Bb, Hh, Dd and Gg, for the manifestation of colour.

R alone produces light red colour on tubers and seedling stems and in the presence of G it produces light red colour on the upper surface of the petals. In the presence of D the intensity of the colour produced by R is increased.

B controls blue colour in tuber skins and seedling stems and it is dominant to R ie, when present alone or in the presence of R it produces blue colour. It alone produces light blue colour but in presence of D the effect of B is intensified. Like R, it also needs the presence of the distributing factor G for its expression on the upper surface of the petals and with G it produces blue colour.

H is an inhibiting factor which suppresses colour formation in the absence of light ie, in absence of light it inhibits the actions of B and R. One dose of H is necessary to inhibit one dose of B or R or RB. D is an intensifying factor which by itself does not produce any colour but in presence of R or B or RB it intensifies their effect. Hence in the absence of D only flushed coloured tubers are obtained with R, B or RB.

G is a distributing factor, presence of which is necessary for the expression of the colour factors on the upper surface of the petals in the flowers. G alone, in absence of any other colour producing factors, produces some red colour on the upper surface of the petals. With D the effect of G alone or in presence of R or B or RB, is intensified.

These factorial analysis suggest that the initial material, used in this investigation are of the following genotypes:--

(1) Solanum simplicifolium :-- BB rr HH dd gg.
(2) Solanum Rybinii :-- bb Rr Hh dd gg.
(3) Solanum Rybinii (C.P.C 979):- Bb, Rr hh Dd GG.

The segregation ratios obtained in the investigation for the single factors and for the factor combinations strongly suggest that the inheritance in these 24-chromosome potato species is of disomic type-

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Discussion.

The possibilities of obtaining resistance to virus diseases in South American and Mexican species of potatoes have been discussed by many authors. Salaman (1921) for instance, found resistance to leaf-roll virus in the species Solanum edinese. Schultz et. al. (1934) reported a positive resistance to virus "X" in the seedling 41956,which is derived from a native cultivated variety of the island of Chiloe. Solanum Rybinii has also been reported on many occasions to be virus resistant.

The type of resistance concerned in this work is that which arises from a hypersensitive reaction of the host plant to infection with a virus. The characteristics of the reaction have been described in detail in previous chapters. In the cultivated varieties of potatoes this reaction has been found to give effective protection against viruses "X", "A", "B" and "C" in the field and varieties endowed with the character are defined as field immune. In South American and Mexican material Cockerham (1943a) has reported that hypersensitive reaction to virus "X" has been found in twenty six clones of five species, to virus "A" in forty one clones of ten species, to virus "B" in thirteen clones of six species and to virus "C" in sixteen clones of six species. He also reported that hypersensitive reaction to virus "Y", which is not readily available in the cultivated varieties, is to be found in the "diploid" species, Solanum simplicifolium, in two clones of the "hexaploid" species, Solanum demissum and in two clones of the "pentaploid" species, Solanum Salamanii (Cockerham 1943a,1946 and 1947).

Cadman (1942) and Cockerham (1943 a.b.) have shown that in the cultivated varieties hypersensitive reaction to viruses "X", "A", "B" and "C" is controlled by single dominant genes, N_x, N_A, N_B and N_C respectively. In this work it has been established that in the "diploid" (2n = 24) potatoes also, hypersensitive reaction to each of the viruses "X", "A", "Y" and "C" is controlled by a single dominant gene. From the nature of the reactions and from the results of the inheritance studied, it seems evident that the same genes which control hypersensitive reaction to virus "X", "A", and "C" in the cultivated varieties are also responsible for hypersensitive reaction to these viruses in the "diploid" potatoes examined in this work. The gene controlling hypersensitive reaction to virus "Y" has been designated as N_Y. It has also been shown that the genes N_X and N_A are strongly linked in the repulsion phase and linkage in the coupling phase, between the genes N_Y, N_C and N_A has also been established.

Segregation in the progenies of Solanum tuberosum (2n = 48) has been interpreted by different investigators on the basis of auto-tetraploidy, allotetraploidy and octoploidy. Cytological evidence has been provided in support of each of these views.

The somatic chromosome number of the cultivated potato has been established as 48 by Salaman (1926), Stow (1927), Fakuda (1927),Rybin (1930), Heyn (1930), Longley and Clark (1930), and Murman and Rancken (1932); and the haploid chromosome number has been determined to be 24. Investigations following the potato expeditions to SouthAmerica and Mexico have brought to light various species with 24, 36, 48, 60 and 72 somatic chromosomes (Rybin 1930 and 1933; Longley and Clark 1930, Müntzing 1933, Hawkes 1944 and Choudhuri 1943, 1944) and have established a well defined polyploid series. Species with less than 24 somatic chromosomes have not yet been found within the genus Solanum. Hence it is assumed that the basic number of chromosome in potatoes is 12 and that the cultivated potatoes are tetraploids.

Earlier workers like Salaman (1910) considered cultivated potatoes as functional diploids. More recently Black (1935) and Collins (1935) have explained the results of inheritance of colour factors on an allo-tetraploid basis. Meurman and Rancken (1932), Ellison (1935) and Ivanovskaja (1939) have put forward cytological evidence in favour of the allo-tetraploid nature of potatoes. That the cultivated varieties of potatoes are of mixed origin has been suggested by Juzepczuk and Bukasov (1929) and Longley and Clark (1930)

These assumptions survived, apparently unquestioned until the publication of Lunden's comprehensive paper (Lunden 1937). This author has analysed the segregation of the genes connected with the inheritance of colour in potato varieties and he has concluded that the segregation was of auto-tetrasomic type. Asseyeva and Nikolaeva (1935) also found evidence of auto-tetraploid inheritance in the potato. Inheritance of pollen sterility (Krantz, Backer and Fineman 1939), resistance to latent mosaic (Stevenson, Schultz and Clark 1939) and resistance to potato scab (Krantz and Eide 1p41) have each been explained on an auto-tetraploid basis. Later Cadman (1942) put forward some new evidence of auto-tetraploid inheritance in the segregational behaviour of the dominant gene N_x controlling top-necrotic reaction to virus "X" in cultivated varieties of the potato. In 1943, Cadman supported his view with ~~the~~ cytological evidence (Cadman 1943).

Although the tetraploid nature of cultivated potato varieties (2n = 48) has been appreciated by most workers, it has been suggested by a number of workers (Lawrence 1931, Müntzing 1933, Schwarz 1937, Ellison 1936 and Choudhuri 1943, 1944) that the basic number of chromosome is less than 12 and Müntzing and Choudhuri have suggested 6 as the basic number. These authors thus conclude that the 24-chromosome potatoes are in fact tetraploids and hence that the cultivated ones are Octaploids. Their conclusion is based largely on the extent of the secondary association of chromosomes at first and ~~the~~ second metaphase of meiosis. This association is assumed to indicate homology of the chromosomes so paired. In the drawings of Longley and Clark (1930 cf. Fig.1d) Lawrence first found the evidence of secondary pairing of chromosomes in "diploid" species of potatoes. This was later confirmed by Müntzing - (1933) in his investigation on the meiosis of "diploid", triploid and tetraploid potatoes and he reported that the secondary association is a characteristic of the potato. Choudhuri (1943, 1944) made a study of meiosis in a wide range of "deploid" potato species and he confirmed the conclusions made by Müntzing. He also suggested that the potato is a good example of a euploid series and that one obvious line of evolution must have been the synthesis of amphidiploid forms of potatoes with higher chromosome number.

The genetic evidence so far obtained from cultivated potatoes disagrees with the theory, that the basic number of chromosome in the potato is 6. A survey of literature has shown up many discrepancies for which the existing theory of secondary association by itself does not seem adequately to account. These theories have been criticised by many cytologists (Claussen 1931, Sax 1931 etc,) and by Cadman (1940 thesis).

Stow (1927) also observed grouping of chromosomes at metaphase but supposed that it was due to an end to end conjugation of non-homologous chromosomes, caused by low temperature. Meurman and Rancken (1932) also found multivalent groups in cultivated potatoes but did not agree that it was due to secondary association.

Very little genetical evidence has been put forward in support of the tetraploid nature of the 24 chromosome potatoes. Choudhuri (1942 thesis and 1944) has reported that the inheritance of certain morphological characters, namely, leaf-shape, stem-wing and flower colour in the 24-chromosome potato species is of tetrasomic type. He suggested that leaf-shape is controlled by two factors L_1 and L_2, the compound leaf character being dominant to the single leaf-character and that the stem wing character is controlled by two factors W_1 and W_2, broad wings being dominant to narrow wings and he further suggested that the factors were inherited in such a way as to indicate allosyndetic pairing. But Choudhuri's genetical data are insufficient to reach any definite conclusion. The interpretation of his data was based on his cytological findings. His genetical results can be equally well explained on the "diploid" basis, if it is considered that single factors are responsible for all the characters analysed by him. Choudhuri suggested that flower colour is controlled by three factors, two being responsible for red and one being responsible for blue. But in the experiments described in this paper it has been shown that a single factor R is responsible for red colour and another factor B for bluecolour. The conclusion which emerges from these data is that the inheritance in these 24-chromosome potatoes is of disomic type for all the genes studied.

It has been established that the gene N_y segregated in disomic fashion and the other three genes, concerned with hypersensitive reaction also seem to behave similarly.

The information required to distinguish disomic and tetrasomic inheritance is supplied by the following tests. Selfing a simplex genotype gives in all the three cases, diploid (Aa), allo-tetreploid ($A_1 a_1 a_2 a_2$) and auto-tetraploid (Aaaa), a 3 : 1 ratio dominants to recessives or nearly so. But in the disomic case ie, in the case of "diploids"and allo-tetraploids, one third of the individuals in the dominant class will be homozygous. On the other hand, in the tetresomic case such non-segregators will be very rare or absent.

It has ~~shown~~ been shown in the previous chapters that in respect of all the four genes N_x, N_A, N_Y and N_C, the segregations of dominants to recessives in the F_1 progenies raised from the cross, dominant x recessive, is approximately of the ratio 1:1. The Plants from the F_1 progenies carrying dominant genes were intercrossed and crossed with recessive and the segregation obtained in these progenies were approximately of the ratios3:1 and 1:1 respectively. It has also been shown that out of thirteen progenies raised from (F_1dominant x F_1dominant)x recessive, two did not segregate, thus showing a significant number of homozygous plants with respect to the gene N_Y in the F_1 intercrossed progenies. These results suggest that the segregation of the gene N_Y is disomic and although similar tests were not applied for the segregation of the other three genes, N_X, N_A and N_C, the results obtained do not depart from disomic expectations. It has also been shown that all the five factors described for the inheritance of colour in these 24-chromosome potatoes segregated in disomic fashion.

A consideration of these findings seems to be quite sufficient to establish that [redacted] ~~in~~ these Solanum species are in fact "diploids", ie, the basic number of chromosome in the potato is 12, and that this basis provides the most useful working hypothesis.

Which ?

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Summary

(1) The hypersensitive reaction shown by Solanum simplicifolium ($2n = 24$) towards viruses "Y" is conditioned by a single dominant gene N_y.

(2) Hypersensitive reactions to viruses "X", "A" and "C" in the 24-chromosome species studied are controlled by single dominant genes N_x, N_A and N_C respectively.

(3) A strong linkage in the repulsion phase between the genes N_X and N_A has been detected.

(4) Linkage in the coupling phase between the genes N_Y, N_C and N_A has also been detected.

(5) The following factors and their relationships have been found to control the inheritance of colour in the 24-chromosome potatoes studied.

R, a red colour producing factor, which alone produces reddish purple colour in tubers and seedling stems.

B, a blue colour producing factor is dominant over R.

H, an inhibiting factor which suppresses colour formation in absence of light. One dose of H is necessary to inhibit one dose of the colour factors, B or R or BR together.

D, an intensifying factor which by itself does not produce any colour but when present intensifies the effects of the colour factors R and B.

G, is a distributing factor, the presence of which is necessary for the expression of the colour factors on the upper surface of the petals. G alone, in absence of any other colour producing factor produces very light reddish purple colour on the upper surface of the petals. With D, the effect of G alone or the combinations RG, BG, BRG are intensified.

(6) It is considered that the 24-chromosome Solanum species examined are all functionally "diploids".

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