POTATO VIRUS DISEASES: REVIEW OF LITERATURE 1941[1]

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Sadasivan (21) conducted at Rothamsted protective inoculation studies with two pairs of related viruses. Tobacco and *Nicotiana glutinosa* plants were inoculated with tobacco mosaic virus or potato virus X^s (which causes necrotic local lesions in the test plants), When the tips of tobacco leaves were inoculated with either tobacco mosaic or X G virus and reinoculated with tomato aucuba mosaic or potato virus X^s, the results showed that the X G-inoculated areas were quite immune from X^s after 12 days, and the tobacco mosaic virus areas were immune from aucuba mosaic after 4 days. The bases of such leaves showed incomplete inhibition even after 20 and 24 days. When the bases of the leaves were inoculated, the results were essentially the same, but the leaf tips acquired resistance completely but much more slowly. When the X^s virus or the aucuba mosaic virus was mixed *in vitro* with healthy plant sap, or with sap containing an unrelated virus, its infectivity was reduced, but this inhibitory effect was much greater when the X^s virus or the aucuba mosaic virus was mixed with its respective related strain. It is concluded that in the plant tissues there is an intense competition among related viruses, and evidence was obtained that the degree of resistance to one is directly proportional to the amount of the other present.

Bawden and Pirie (5) secured experimental evidence that four viruses—tobacco mosaic, potato X, tomato bushy stunt, and tobacco necrosis—were irreversibly denatured by urea. For each virus there was a critical concentration of urea, below which no irreversible effect was exercised on infectivity. Inactivation of tobacco mosaic virus and potato virus X, but not that of the remaining two viruses, was accompanied by separation of the nucleic acid from the protein.

Bawden and Pirie (6) also conducted experiments to determine

[1]Pathologist.

[2]Not all papers included in this report were read in their original form: in many cases only the abstracts appearing in the *Review of Applied Mycology* were used.

the effects of alkali, sodium dodecyl sulphate, urethane, guanidine, pyridine, picoline, lutidine, aniline, nicotine, phenol, sodium salicylate, sodium benzoate, and sodium hippurate on the viruses of tobacco mosaic, tomato bushy stunt, and on potato virus X. The effect of alkali on tobacco mosaic is complex; treatment at pH 9.3 may cause increase of infectivity, a pH 10.5 loss of infectivity but not serological activity, and at pH 11 total loss of all characteristics. In the presence of alkali, sodium dodecyl sulphate readily destroyed the virus, separating the nucleic acid from the protein. Except nicotine and arginine, which formed with tobacco mosaic reversible fibrous precipitates, all the substances tested (at concentrations below 4 M) inactivated the viruses in neutral solutions.

Gulyás (11) found that the Y-virus in potato plants moves at the rate of 6 to 8 cm. in 3 to 4 days, the X-virus more rapidly, and the leaf curl covers 25 to 30 cm. in 8 to 12 days. An examination of fixed material revealed spherical X-bodies 3 to 25 Y in diameter, in various parts of Y- and crinkle-infected plants, a diseased cell usually containing one such element, though two or three were occasionally present. In certain infected cells, particularly those in proximity to X-bodies, or to vacuolated cells, 8 to 12 green granular bodies developed giving a plasmodium-like appearance. In such cells the chloroplasts turned dark yellow, or pale yellow-green, with a consequent disturbance of their normal functions.

Kohler (16) isolated three strains of the tobacco ring-spot virus from potatoes affected by a yellow spotting of the foliage, namely, (1) from a single plant of a stand comprising 50 plants of the Edelgard variety, designated "Ede;" (2) from a plant of a Pomeranian selection, "Po;" and (3) from several plants of the Frühmölle variety, "Früh." The type of spotting on the last-named variety was of a strikingly large pattern agreeing in all essentials with the North American calico, though obviously caused by a different virus. On the Edelgard and the Pomeranian plants the symptoms resembled those of aucuba mosaic. The effects of inoculating Turkish tobacco (Samson and Xanthia) with these three strains from potato were at first inconspicuous, but gradually acquired the intensity of a typical severe attack of ring rot. Only a few of the cucumber plants inoculated by rubbing with the three ring-spot strains developed systemic infection, though all reacted by the formation of pale green spots of the needle-prick type. The "Ede" and "Po" virus strains produced divergent symptoms on bean, *Phaseolus vulgaris*, leaves, those due to the former consisting merely of isolated sunken, necrotic spots, whereas the latter caused the formation of numerous circular, reddish-brown, necrotic zones, followed by shedding of the inoculated leaves and in some cases by the brown discoloration of the stem and ultimate collapse of the plants. Extensive necrotic lesions, merging into chlorotic patches, and succeeded by a prominent yellow mosaic spotting, developed on inoculated *Nicotiana glutinosa* leaves. Pepper, *Capsicum annuum,* leaves reacted to the virus, especially to the "Po" strain, in an unusual and interesting manner; the delayed necrosis involving the petioles, leaf blades, and veins is apparently directly due to a toxin formed in response to the invasion of the stem apex by the virus. The thermal death point of the "Ede" and "Po" strains of the ring-spot virus was found to be 63° C. The "Früh" strain tended to be more heat-resistant. The two first-named strains were still infective at dilutions of 1:100, but not at 1:1,000, corresponding in this respect somewhat to Price's ring-spot virus strain. "Früh" strain caused some infection at 1 in 1,000. This corresponds to Price's strain No. 1. Inoculations with the "Früh" or "Po" strains were experimentally shown to protect Samson tobacco plants against subsequent infection by the "Ede" strain.

Offermann and Victoria (19) studied the serious potato disease presumably caused by Solanum virus 1 (potato virus X) which is liable to be confused with early blight, *Alternaria solani.* The dark, concentrically zonate foliar lesions are common to both. The symptoms of the virus, however, occur on the young tissues and are confined to the upper side of the leaves, whereas the fungus attacks the older leaves and involves both leaf surfaces, causing a severe necrosis of the veins. The virus also affects the stem and tubers, and produces a necrosis of the terminal buds and eyes. The virus causes symptoms on tomato very similar to those of spotted wilt. The two viruses may be distinguished by their reaction to mercuric chloride, which at a strength of 1 in 1,000 immediately inactivates the spotted-wilt virus, whereas potato virus X retains its virulence when in contact with the disinfectant for 5 days.

The virus was purified according to Bawden and Pirie's technique.

Valleau (28) made a comparative study of the host range and physical characters of the tobacco streak and potato yellow-dwarf viruses and indicates that they are similar, possibly merely strains of one virus. Tomato and potato, previously believed to be immune, were found to be hosts of tobacco streak. Potato yellow dwarf is known to affect red clover *Trifolium pratense*, and circumstantial evidence indicates that the streak virus is transmissible from sweet clover *Meliotus alba,* to tobacco. The symptoms produced by the two viruses are not identical either in tobacco or in *Nicotiana rustica*. In tobacco the yellow-dwarf virus causes vein-clearing and no streak. Tobacco with systemic yellow dwarf developed a combination of symptoms on inoculation by grafting with the streak virus. The author concludes that the fact that the streak virus does not afford protection against yellow dwarf does not necessarily point to a difference in identity.

Price and Black (20) carried out cross-protection tests in an attempt to clarify the relations between tobacco streak and the potato yellow-dwarf virus. Artificially infected *Nicotiana rustica* plants showing the systemic stage of tobacco streak failed to develop further symptoms of streak when inoculated with the severe strain of potato yellow-dwarf virus, with tobacco mosaic, tobacco necrosis, or with tobacco ring-spot; the plants in each case developed symptoms characteristic of the given virus. Of the plants systemically infected by yellow-dwarf, those inoculated with the severe strain of potato yellow-dwarf virus failed to develop further symptoms of yellow-dwarf, whereas those inoculated with tobacco streak or any of the other three viruses previously used, developed local lesions typical of the virus used as inoculum. These results indicate that plants affected with tobacco streak are not protected against potato yellow-dwarf virus, and it is concluded therefrom that the two viruses are not strains of the same virus, and in this sense are unrelated. Furthermore, the other viruses used do not seem to be related to each other.

Hansen (12) discusses the various systems of naming plant viruses. A list of the synonyms for the European potato viruses is given, as well as a collection of common synonyms for potato viruses. Most of the names for the diseases other than Danish refer not only to the clinical picture but also to the causal viruses. The Danish names, however, correspond only to the symptoms and are in no way connected with any of the causal viruses.

Hansen (13) discusses in detail the relationship between potato viruses and their ways of transmission. The writer does not believe that transmission of virus X can be explained by wind mutilation of leaves, and is inclined to believe that auto-infection plays an important part. A fully tabulated account of the experiments in Denmark is given, comprising infection experiments in the field in 40 different localities in 1938, 1939, and 1940. The dispersion of virus-Y infection within the individual plots was practically identical in the eastern and western parts of the country. There was an average of approximately 1.5 times more infection in the rows that were quite close to the Y rows than in those a row farther away. Shelter from the wind had a rather marked effect on the amount of infection, but the effect varied with the other general conditions for infection. In special infection experiments with tobacco, as well as with potato plants, it was found that a considerable amount of infection took place about the middle of July in 1938. In 1939 the time for infection was somewhat later, and in 1940 it was still later. Much more virus infection was found in the immediate neighborhood of towns and of the coasts, and near marsh or other coast-meadows, than in corresponding areas at some distance from these localities. A high degree of positive correlation was found between the mean temperature in July and the infection percentage, but the line of regression was not straight. The above-mentioned factors influenced aphid population.

Black (7) in his studies on hereditary variation in the ability of the clover leaf hopper to transmit potato yellow-dwarf virus found that selective breeding through ten generations resulted in the development of two races of clover leaf hopper, *Aceratagallia sanguinolenta,* one active and the other inactive. Under conditions in which 80 per cent of the active individuals transmitted the potato yellow-dwarf virus, *Marmor vastans,* to crimson clover *Trifolium incarnatum,* only 2 per cent of the inactive insects and 30 per cent of the hybrids between the two races passed on the infective principle. Active individuals appeared in colonies of the inactive race, whereas, conversely, some inactive ones were present among the active. Active insects from an active race were more efficient vectors than those from an inactive race; a significantly higher percentage of males than of females transmitted the virus.

Black (8) found that leaf hoppers, *Agallia constricta,* collected in New Jersey carried a strain of the potato yellow-dwarf virus, *Marmor vastans.* This strain differs from the variety *vulgare* originally described from New York State and transmitted by another Agallian leaf hopper *Aceratagallia sanguinolenta.* The differences in the effects produced by the two viruses on crimson clover *Nicotiana rustica, N. glutinosa,* and *Solanum tuberosum* were minor but nevertheless consistent and easily recognizable. In two experiments the New Jersey virus protected *N. rustica* plants against the lethal variety of the New York virus. Because of the specific transmission of the New Jersey virus by a species of Agallia, it is proposed that it be named *Marmor vastans* H. var. *Agallia,* Nov. var.

Heinze and Profft (15) found that *Myzus persicae* is the only one of the potato-inhabiting aphids which is of any practical importance as a vector of viruses in Germany, though *M. pseudosolani* may occasionally be implicated in the transmission of leaf roll. Studies on the migration of potato aphids were conducted at Dahlem, Berlin, representing a locality where there is generally rapid spread of virus diseases, and at Dromburg, East Pomerania. The increase of the insects was found to be favored by periods of fair weather, especially during April, and from May to mid-July. High winds bring the aphids out of their winter quarters, and light, dry breezes promote their movement from plant to plant. The disastrous early infestation by *M. persicae* was less prevalent at the Pomeranian Station than in the Berlin district because of the relatively late appearance and dispersal of the aphids at the former site.

Because of the over-wintering habits of *M. persicae,* the writers recommend at least one dormant spraying of peach and apricot trees.

Heinze (14) cites official statistics in support of his statement concerning the rapid and widespread extension of peach and apricot cultivation during recent years in Germany, a development calculated, if allowed to proceed unchecked, to terminate the production of healthy stocks of seed potatoes, as the aphid *Myzus persicae,* which is responsible for the transmission of potato viruses, overwinters on these fruit trees. Störmer's warning (the Mitt. Landov., Berlin 904-906, 1937) that no naturally healthy potato-growing regions would be left in Germany within a few years, owing to the fact that the progress of degeneration from west to east failed to receive the necessary attention, may well be realized unless a drastic limitation on peach and apricot growing is enforced, at any rate along the north German coast for a distance of approximately 150 km. inland.

Sandford and Clay, (23) report that during the last 10 years a potato disease apparently hitherto undescribed, and for which the name "purple dwarf" is suggested, has developed in many fields in southern, central, and north-central Alberta. It seems to affect all districts equally, but has not so far seriously reduced yield. The number of affected plants seldom exceeds 1 per cent and although infection has reached 5 per cent in a few cases, many fields appear to remain unaffected, although infection has reached 5 per cent in a few cases. All varieties seems to be susceptible.

Plants affected with purple dwarf are readily recognizable as they emerge from the affected seed pieces, being stunted, rigid, brittle, and frequently dark green. The sprouts may remain abortive and die. General stunting and distortion, with the early development of a purple color, especially on the margins of the apical leaves, are invariably present under field conditions. The underground parts are at first apparently normal, but before long the older roots, then the stolons, and finally the epidermis of the lower stem turn brown and decay, discoloration starting at the extreme base of the stem and spreading outward through the roots and stolons and upward through the stem. The outer part of the brown roots and stolons may easily be slipped off. Tubers from affected plants are seldom over 1 inch in diameter, and, as a rule, only very few small ones or none develop. These tubers always show severe necrosis. The stolons and tubers give no secondary growth, and the old seed piece usually remains sound.

Under field conditions the pith of the stem is normal green to darker green in color, and remains sound until the disease is well advanced, when general disorganization may begin at the base of the stem. In the tuber and upper stem the pith usually remains normal. The phloem throughout the stems, stolons, and roots is discolored and often plugged with a material, that is stained deeply with Sudan III. A distinct browning of the outside of the vascular cylinder is a characteristic symptom in the lower stem, stolons, and roots. Experimental evidence and field observations strongly indicate that transmission occurs through affected tubers. The condition was transferred to the stems of healthy potato plants by inserting in them pieces of petioles from affected potato plants. Furthermore, the tissue of purple-dwarf plants yielded neither bacteria nor fungi. On this basis, the disease is considered to be of virus origin.

In addition to leaf roll, in potato samples from Silesia, Mark Brandenburg, Saxony, and Berlin; Kohler (17) found on examination at the Biological Institute, Dahlem, that some of these were infected by a virus transmissible by means of *Myzus persicae* and by grafting, but not by mechanical juice transfer. In the field the virus appears to be virtually latent, but in combination with other viruses, it causes severe crinkle, sometimes accompanied by stunting. In greenhouse plants the first symptoms of the disease are a pronounced upward rolling of the leaflets, similar to that found in leaf roll but usually only temporary. The leaves, moreover, remain soft and pliable and do not develop the chlorosis characteristic of leaf roll. In the Altgold and Wohltmann varieties the longitudinal growth of the shoots becomes accentuated, whereas in Altgold and Ackersegen the leaves are abnormally small. The foliage displays a faint, diffuse, yellowish-green tinge originating in the mild and lateral veins of the pinnae, and imparting to the entire plant a somewhat lighter aspect than that of normal stands. Anthocyanin spots are produced on the rolled leaves of Parnassia and Wohltmann. As severe crinkle is a typical sympton of the virus in mixed infections, the designation K (Kräusel) is proposed for it.

Bald and Norris (1) studied the effect of the latent virus (virus X) on yields of potatoes. After stating that almost every plant of the six most commonly grown potato varieties in Australia appear to carry at least one strain of potato virus X, the authors describe an experiment carried out in 1939-'40 to determine the effect of the presence of this virus on yield. The seed tubers used were of the President and Factor (Up-to-Date) varieties. The latter were derived from a single tuber which some years previously had been found free from virus X. Before planting, the clean and infected tubers were indexed by inoculating from each to pepper, *Capsicum annuum* plants. These tests confirmed the presence or absence of the virus and demonstrated that the isolates were of average severity. The experiment was arranged so that the unit sub-plot consisted of three plants. Four sub-plots (President with and without, and Factor with and without virus X) were randomized in a group along a row, similar rows occurring four times in each of five long rows. Between adjacent sub-plots single clean President or Factor plants were set to reduce current-season infection between adjacent affected and healthy plants.

During the season no symptoms of virus X were noted on any plant, and no differences in vigor or growth habit were observed between healthy and affected plants of the same variety. In all, 182 plants grew, of which 90 were Factor and 92 were President. The mean yield per plant was 142 and 172 grams, respectively, for infected and clean President, and 148 and 240 grams, respectively, for infected and clean Factor. Thus the mean loss in yield resulting from infection was 30 per cent. The authors concluded that these results support the opinion that virus X is one of the main causes of the reduction in yield of potatoes in Australia. However, as the effects of the virus are spread evenly over the crop, they escape notice.

Bald, Norris, and Dickson (2) studied a disease of Factor potatoes in New South Wales that was diagnosed as spindle tuber. Three stages in tuber growth were differentiated by means of logarithmic curves based on measurements for sound and infected plants, and the following characteristics were noted in the diseased tubers: (1) The rudimentary tubers formed from the stolon tips are of abnormal shape, but smaller than those produced by healthy plants; (2) growth is uniform in all dimensions, from approximately 0.75 to 2.5 cm. in length, causing less expansion in this second stage than occurs in normal material; and (3) following a transitional period between the second and third stages, growth appears to follow a comparatively normal course, but as apical growth begins in the diseased tubers, these are narrower in cross-section than sound ones of the same length. An analysis of the measurements made on Green Mountain tubers by Schultz and Folsom and on Bliss Triumph by Werner gave results similar to those obtained from Factor potatoes.

Scott (24) carried on investigations to obtain statistical information of the effect of the various types of mosaic disease, leaf roll, and wilting upon the yield of potatoes in Scotland. Slight mottle, usually caused by mild strains of virus X, but sometimes due to virus A, may reduce the yield by 16 to 25 per cent. Mild mosaic, generally caused by virus X, but occasionally by Virus A in combination with virus X, may reduce the yield by 30 to 40 per cent. Severe mosaic caused by virus Y alone or in combination with A or X may reduce the yield by 75 to 90 per cent. Severe mosaic increases two- to threefold, and leaf roll fourfold from year to year. Methods of controlling the mosaic group comprise the use of varieties virtually immune from viruses A and Z, the planting of the highest grade seed, adequate isolation, and thorough roguing, especially in the early part of the season.

Bald and Norris (3) state that it may be assumed that more than 90 per cent of the potatoes grown in Australia are infected by virus X. The losses from virus X appear to be at least as heavy as those from all other diseases combined. A virus-free Up-to-Date tuber was found. This tuber has been grown and the yield tested for freedom from virus X. The progeny of this tuber is being propagated to develop a possible virus-free stock to replace the infected stocks grown at present.

In a report on agricultural features of the Australian potato industry Bald (4) states in the section on potato diseases that losses caused by diseases (excluding latent mosaic) in Australia approach or exceed 20 per cent of the potential yield. The following conservative estimates have been made for percentages of losses incurred through preventable virus diseases (comprising all except latent mosaic) in the most widely grown varieties: Carman, 31 per cent; Brownell, 26; Up-to-date, 18; Snowflake, 4; Delaware, 6; Bismarck, 8; and miscellaneous, 7.

Schultz, Clark, and Stevenson (26) have shown that on the basis of symptomatology the reactions of potato seedling varieties to virus X may be classified as (a) symptomless carriers, (b) necrotic, (c) light green and slightly rugose, and (d) faintly mottled. On the basis of resistance to virus X, the varieties may be grouped as (a) immune

(b) rarely infected, and (c) easily infected. The corresponding reactions to virus A may be expressed on a basis of symptoms as (a) necrotic, (b) pale green and rugose, and (c) mottled; whereas on the basis of resistance to virus A, the varieties are grouped in the classes used for virus X. The resistance reaction of the parents to virus A or X is transmitted to a light percentage of the progeny of crosses, es pecially in the case of two resistant parents. Earlaine, Katahdin, and S. 24642 are immune from virus A by aphid infection but susceptible to it by grafting. These varieties apparently segregate for resistance and susceptibility to virus A in crosses with non-resistant varieties. Progenies of virus-X-immune X virus-A-immune have been developed that combine immunity from both viruses and should play an important part in the control of mild mosaic, of which these viruses are components.

Loughnane (18) describes two experiments conducted in Eire in 1937 and 1938 in which healthy tubers of different varieties were grown near a field in which cabbage had been planted and were exposed to natural infestation by *Myzus persicae.* The results obtained showed that the most susceptible of the varieties tested for leaf roll were Arran Cairn, Up-to-Date, and Arran Signet; intermediate in susceptibility were Arran Pilot, British Queen, Kern's Pink, Gladstone, Arran Peak, Arran Victory, Dunbar Yeoman, Ulster Monarch, May Queen, President, Great Scot, Arran Crest, Epicure, Redskin, and Dunbar Standard; and least affected were Flourball, Arran Bonner, and Majestic. Yield was reduced by at least 80 per cent in King Edward, President, May Queen, Arran Crest, Arran Pilot, Arran Signet, Redskin, and Dunbar Yeoman; between 50 and 80 per cent in Epicure, Arran Cairn, Dunbar, Standard, Ulster Monarch, Arran Banner, Eclipse, Gladstone, Arran Peak, British Queen, Kerr's Pink, and Arran Victory; and by 50 per cent or less in Up-to-Date, Great Scot, Majestic, and Flourball.

The evidence demonstrated that the effect of disease on yield is directly proportional to the effect on vigor. On the whole all the early varieties showed a serious reduction of yield when attacked: in main-crop varieties there was wide variation in the effects on vigor and yield, but a serious loss of yield followed extreme reduction of vigor.

In the 2 years of the test initial infestation by *M. persicae* took place on the 12th of May, and maximum infestation about mid-June. It was found that even when vectors and sources of leaf roll are present in a potato crop in rather large numbers, there is a significant difference in the extent of the spread of the disease to healthy plants growing at varying distances from the source of infection; healthy plants in proximity to the source are more likely to become infected than those removed from it by a distance of one or two rows.

Samuel (22) reports that certificates issued by the Ministry of Agriculture and Fisheries after inspection of growing crops of potatoes in England and Wales now take into consideration the health, as well as the purity, of the crops, which have to comply with two conditions: (1) The seed planted must be class 1, and (2) the crop must be grown at least 50 yards away from any other potatoes not eligible for entry under the first condition. These conditions are intended to assure that the stock is of good standard of health and that it was grown in some degree of isolation from outside sources of infection. It is emphasized that the aim of the English scheme is to indicate those stocks that are likely to have maintained their health to a satisfactory extent during their first year of growth for seed production. The author briefly summarizes the chief factors affecting the health of seed potatoes in England and discusses the spread of virus diseases within the field and spread into a field from outside sources. A good example of the latter was observed in Kent in 1938 when leaf roll spread from one corner of a field; the source of infection was possibly an adjacent cabbage field that had been cleaned up soon after the potatoes had been planted. Similar spread of leafdrop streak (potato virus Y) has also been observed. He considers it advisable not to plant potatoes adjacent to an overwintered Brassica crop. The destruction of the potato tops before the time of natural dying tends to produce more healthy seed, but it reduces the yield.

The Department of Agriculture for Scotland (9) has issued a register divided into four parts which shows in alphabetical order (1) the varieties, (2) the counties where grown, and (3) the growers of the crops.

Part I (T.S.(A)), seed true to type, immune from wart, and (N.I.(A)), seed true to type but not immune from wart, include crops that were inspected during the growing season and certified by the Department to attain a standard of purity of not less than 99.5 per cent and to contain not more than 1 per cent virus diseases, including not more than 0.5 per cent in all of leaf roll, severe mosaic, and wilding (witches' broom).

Part II (T.S.(H)), seed true to type, immune from wart, and Part IV (N.I.(H)), seed true to type but not immune from wart, include crops that were inspected and certified to be true to type, to attain a standard of purity of not less than 99.5 per cent, and to contain not more than 3 per cent of leaf roll, severe mosaic, and wilding.

All crops included in the Register are the subject of a certificate to the effect that wart disease has not been known to have occurred on the land in which they were grown.

Another register (10), a supplement to the register of potato crops inspected and certified "T.S.(A)", "T.S.(H)", "N.I.(A)", and "N.I.(H)" during 1941, shows in alphabetical order the varieties and growers of crops that were found to be 99.95 per cent pure and true to type and to contain not more than 0.25 per cent of virus diseases and wilding, including not more than four plants per acre leaf roll, severe mosaic, and wilding.

Tamargo (27) reports that after 3 years' observations at the Agricultural Experiment Station, Santiago de las Vegas, Cuba, most of the potato seedlings and varieties introduced for trial purposes tended to lose their native vigor in their new environment on account of climatic influences (short days) and virus diseases. Some resistance to mosaic was shown by Alma, Hindenburg, Oldenwälder, Blaue, and Weltwunder, whereas Duke of York, Gloria, Hetman, and Jubel were highly susceptible.

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