THE IMPORTANCE OF POTATO VIRUS X[1]

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Although it is generally accepted that potato viruses are of serious economic importance when they cause obvious systemic diseases in commercial varieties, there has not been such a ready acceptance that barely perceptible foliage diseases from similar causes can also cause economic loss. Potato virus X is the most ubiquitous of the potato viruses and certainly the most insidious. Yet to many who are intimately concerned with potato culture, it is still a pathogen of doubtful importance because its effect upon a growing crop is not so obvious as that caused by potato virus Y or the leaf roll virus. We associate virus X with diseases that are barely perceptible and not worthy of control, and yet it is the one potato virus that can be most easily controlled by specific breeding.

It has been shown that virus-X infections that do not cause apparent diseases may still reduce the total weight of the crop (15, 18, 19, 20). In fact, reduction caused by symptomless infections of potato virus X was sufficient to initiate virus-X-free certification schemes in many countries (1, 14, 16, 19, 20). But despite these experiences in some countries there is general belief in others that loss in weight of crop can only be detected when plants show definite symptoms of disease (5, 6). Results on work with stocks free from virus X and stocks infected with symptomless strains of this virus did not show appreciable differences (2). This similarity in weight of crop may have been due to intensive selection within commercial stocks for local environment (2, 14, 15). Variations within varieties that affect foliage type and tuber yield are common, and lines infected with virus X can be selected to outyield other lines that are free from the virus (1). Experience has shown that with certain varieties it is almost as difficult to maintain stocks true to a type as it is to maintain them virus-free (14). The decrease in yield caused by variations within a variety can be similar to that caused by a virus disease. But when it cannot be clearly shown that reduced yield was due to a single cause, a grower is usually not interested. Even if slight differences due to virus infection could be detected, they would receive scant attention when there are wide fluctuations in prices paid to potato growers from year to year.

Although assessment of virus disease for seed certification is made by interpreting visible symptoms in a growing crop, intensities of the mosaics caused by virus X may vary during a growing season. Similarly, plants growing from the same source of infected stocks may show symptoms in one area and not in another. This is probably why 23 of the 26 certification schemes in operation in North America do not include simple mosaic in certification requirements.

STRAINS

Single strains of virus X are rarely found in the field as natural infectors. In fact, it is doubtful whether a truly single strain can be obtained by methods presently used. Under some conditions isolations and re-

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isolations by dilutions and local lesions that eventually are considered to be single strains may show themselves to be strain mixtures. Different potato seedlings may select different infective portions from an isolate that is being used as inoculum of a presumed single strain (11). Inoculations to *Datura stramonium* v. *tatula* with virulent strain may cause mild symptoms after passage through a succession of plants; and similarly mild strains may cause severe symptoms.

Field observations

Surveys of areas where table stock is grown from seed brought in at intervals of several years have revealed that there was a sharp increase each year in the number of plants with severe mosaic. Symptoms indicated that diseases were probably caused by either of the aphid-borne viruses A or Y, and virus X. However, in most cases tests showed that severe symptoms were caused by a dominance of severe strains of virus X alone (4). The varieties observed, Green Mountain and Netted Gem, are known to have been infected with virus X for many years.

In these surveys, cases of severe mosaic in single stems of otherwise healthy-looking plants were relatively easy to find (Fig. 1). Inoculations from symptomless parts of such plants usually caused mild non-necrotic symptoms of virus X on *D. stramonium* v. *tatula.* Inoculations from leaves on the severely diseased stems caused distortion and necroses of the same indicator plant (Fig. 2). Changes of this kind were first observed as severe mosaic in one compound leaf on a stem. An immediate test on D *stramonium* v.*tatula* plants indicated that a severe isolate of virus X dominated this severely diseased leaf, and a mild one dominated the rest of the plant. This severe disease then developed progressively from leaflet to leaflet in each of the remaining leaves on that stem (Fig. 3). Within three weeks of the first observation on the single leaf the whole plant was dominated by the severe strain, and symptom development had been followed from leaflet to leaflet within each leaf, from leaf to leaf on each stem, and from stem to stem.

Tubers were harvested from the foregoing plants and planted in the following spring. They were cut and planted to produce four plants from each tuber, and the shoots were observed as each plant came above ground. In most cases, one, two, or three plants from each parent tuber showed severe mosaic from the earliest stage of growth. Plants produced by each of the other parent tubers were either entirely symptomless or showed severe mosaic in all parts of the plant. All plants were tested and found to be infected with virus X alone.

Though movement of severe-strain virus particles to and within the tubers of these plants was comparable to movement in foliage, severe strain dominance was not always accomplished before the tubers were harvested and stored. According to MacKinnon and Munro (12), little movement of virus X takes place in potato tubers during storage.

These changes from symptomless infection to severe diseases are usually assumed to be caused by strain mutations. But although there may be a high frequency rate of mutation in potato mosaic viruses, it does not necessarily mean that strain mutation is always the cause. Severe mosaic that appears only in one stem of a field plant seems to arise when the weather has been variable. Delay in growth has been followed by a

FIG. 1.—Severe mosaic of single stem in an otherwise symptomless plant.

surge of growth and consequent sudden mass increase of virus particles. Under these conditions mutations may arise, but strain dominance may also change and the mild strains that formerly dominated and controlled the symptoms may be dominated in turn.

Under these unstable conditions, then, the principle of cross-protection does not hold. But even though this may not be commonly known, the doubt with which its practical value has been handled suggests that it is suspect. This attitude together with the practice of raising seed potatoes free from virus X in Holland, Germany, South Africa and Scotland indicates a tacit acceptance that cross-protection is unreliable.

CONTROL

Some strains of virus X tend to cause relatively severe diseases in most potato varieties, and others cause relatively mild diseases in the same varieties. Other seedlings and varieties become infected by isolates from within the mixture of strains that are contained in natural inocula. Some select strains that cause a mild disease, some select strains that cause a severe disease, and others appear to accept the complex (11). It has also been shown that some strains, selected for use in protective inoculations, do not infect certain seedlings. The same seedlings, however, become readily infected when the inoculum contains other strains. Such characteristics are found in seedlings from specific crosses (11).

Varietal resistance

Despite the tendency of some seedlings to be selective in acceptance of strains of virus X, potato plants have an overall inherent degree of resistance or susceptibility to the virus. A seedling therefore, may be assessed according to the ease or difficulty of becoming infected after inoculation, and by the consequent reaction after infection. It may be

FIG. 2.—*Datura stramonium* v. tatula: left, inoculated from symptomless stems, right, inoculated from stem with severe mosaic.

FIG. 3.—Severe mosaic developing from leaf to leaf in potato plant.

susceptible or resistant to infection, and tolerant or intolerant when infected. This of course excepts seedlings selected for immunity to this virus obtained in progeny when one of the parents is U.S.D.A. seedling 41956 or one of its derivatives.

The terms susceptible and resistant to infection relate to the same phenomenon. They refer to the ease or difficulty of virus entry and movement within a plant after natural inoculation.

Tolerance and intolerance are general terms that refer to the results of reaction between cell and virus and the consequent effect upon the plant as a whole. It may be that in each kind of cell there is a critical stage in the reaction between cell and virus or in virus multiplication. When this critical stage is reached there is cell breakdown indicated by mosaic, cell destruction indicated by necrotic streak, or both. In these cases the plants are considered to be intolerant to the causal virus or virus strain. If then the plant is tolerant, the critical stage is not reached, because of impeded multiplication or of a parasitism almost akin to symbiosis.

Although the relationship to resistance and tolerance cannot always be predetermined between plant and virus, there is a specificity of reaction of plant to virus strain, and of virus to cell type. Seasonal changes and other environmental effects also appear to hasten or retard development towards the critical stage.

Field resistance

When resistance to infection and intolerance when infected are combined in the same host, the plant is considered to be field-resistant. Katahdin is an example of a variety that has this kind of resistance to the potato-mosaic viruses. Such varieties are probably readily accepted by growers when field-resistance includes a number of pathogenic diseases. They are considered to be 'easy to grow'. However, diseases caused by strains of virus X can best be prevented by breeding for field-immunity (8) or for immunity (21).

Field immunity

One of the fundamental differences between Old World potato varieties is in the way they react when grafted with a scion infected with any one of the potato viruses X, A, B or C (Fig. 4). Some are killed with top necrosis whereas others develop nonnecrotic symptoms. If some leaves of a plant that reacts with top necrosis to a specific virus with this graft method are rubbed with inoculum of that virus, necrotic local lesions develop on the rubbed leaves. This reaction is an efficient form of immunity from the causal virus under natural conditions of infection, and varieties that react in this way are described as being field-immune (7). These reactions that distinguish varieties are due to simple genetic differences. Cadman (3) has shown that the necrotic reaction to virus X is controlled by the gene Nx, and that all varieties carrying this gene are field-immune to all strains of virus X except X_B and its variants. There is also a linkage between Nx and Na, the gene that operates similarly in response to potato virus A (10).

The top-necrotic reaction is important when it is a rarity in the field, and the expression field-immune is apt. But sometimes a natural infection is not localized to the inoculated leaves, and when this happens the plants are killed by a systemic necrotic disease. Tubers set by such plants may show necrotic lesions or areas (Fig. 5). Eyes become necrotic and many fail to sprout; those that do, give rise either to healthy plants or to plants that become necrotic and die before tubers are formed. The

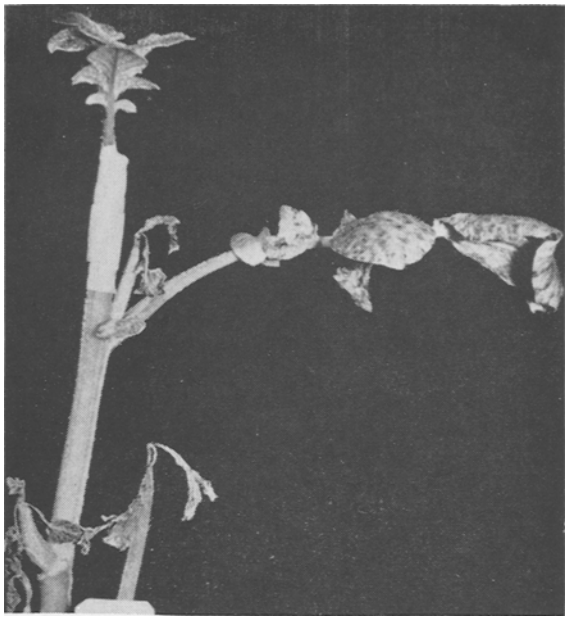

FIG. 4.—Top necrosis of a seedling caused by virus-X-infected scion.

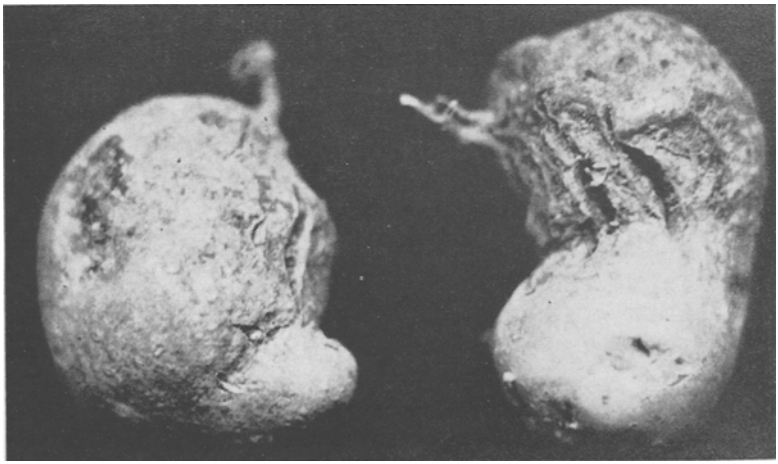

FIG. 5.—Tubers with necrotic lesions; harvested from plant destroyed by top necrosis.

frequency with which this occurs depends upon the variety and is probably due to extreme susceptibility to infection. According to Cockerham (10), varieties with a low degree of resistance, such as Arran Crest, show a greater proportion of necrotic systemic infections in the field than varieties with a high degree of resistance, such as King Edward. In any case, these infected plants are self eliminating in the field for the reasons outlined. .

Immunity

Although there is some doubt as to whether U.S.D.A. Seedling 41956 is immune or just extremely hypersensitive to virus X (17), there has been no report of this seedling or any of its selected derivatives being found in the field with an apparent disease caused by this virus. For all practical purposes, seedlings that react to inoculations with virus X in a similar way to that of U.S.D.A. Seedling 41956 are immune.

Growers' acceptance

A generalized field resistance to infection by potato disease pathogens seems to have been responsible for the popularity of certain varieties before specialized demands for processing became widespread. Certainly, immunity in the field to one or two viruses alone has not been and is not, sufficient to obtain growers' acceptance. Although the varieties Saco and Tawa are immune to virus X, they will, like Craig's Defiance which is field-immune to viruses X, A, B and C, rise or fall on other merits. In the production of new varieties not intended for specific purposes such as extreme earliness or processing, no one single quality is required any more than another. An attractive domestic variety of good culinary quality that produces commercial sized tubers fairly early may fail on the basis of extreme susceptibility to any one of the causes of major economic disease. Similarly, a variety with resistance to one or more specific pathogens may not be accepted because it lacks other major qualities demanded in a potato. There is no doubt that requirements in a potato variety include disease resistance, ease in culture and good cooking qualities.

Breeding of commercial varieties in West Germany has always been largely done by private breeders (13). This custom is to introduce a new variety that is superior in at least one respect, and equivalent in all others to the variety it will replace. Whether or not the replaced variety should go completely off the seed-potato market, may be a matter for debate; but the important thing seems to be that of progressively adding qualities to those already obtained. Unfortunately, many improvements are in degree and consequently not always apparent. Perhaps the greatest advantage of breeding for immunity or field-immunity to potato virus X is that, when obtained, it has been brought about by major genes and is a clearly recognized characteristic of the seedling.

The factors that determine the choice of breeding for immunity over field-immunity to potato virus X and vice versa are probably few. There are two in favor of field-immunity. Reference has already been made to the linkage between genes Nx and Na; the other is the greater possibility of obtaining earliness, good agronomic, and good culinary qualities. Cockerham (9) has shown that there is a wide range of possible parents with field immunity carrying many different combinations of other desirable qualities, whereas breeding for immunity is restricted to the use of U.S.D.A. Seedling 41956 and its derivatives as one parent. On the other hand the main possible weakness in field-immune seedlings is that of being extremely susceptible to the virus. When lethal necrosis of a potato plant caused by virus X is seen in the field for the first time, the observer is usually in doubt both as to its cause and its relative importance. But he need not be concerned, because the phenomenon is rare, it is self-eliminating, and it is abnormally conspicuous in relation to the actual number of such plants that could or would be in a growing crop.

Summary

Severe mosaics caused by potato virus X alone are commonly found in potato crops where new seed replacement is infrequent, and the varieties grown are wholly infected with the virus. These severe mosaics often arise in single stems of otherwise symptomless plants and spread rapidly through leaves of each stem until all foliage is showing severe symptoms. The rapid movement of a strain, newly arisen either by mutation or host selection, through parts of a plant already infected with that virus nullifies the principle of cross-protection.

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