Infection of tomato seed by different strains of tobacco mosaic virus with particular reference to the symptomless mutant MII-16

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Abstract

Eight different strains of TMV were used to inoculate tomato plants when the first truss was in flower. The proportion of the seeds infected by TMV was highest with the enation strain followed by tomato and winter necrosis strains. The other strains, viz. yellow ringspot, yellow mosaic, crusty fruit and tobacco strains and the symptomless mutant MII-16, either resulted in a low proportion of seeds with TMV or none at all. MII-16-inoculated plants consistently gave the lowest proportion of TMV-infected seeds. The possibility of using this strain to produce virus-free seeds is discussed.

Additional keywords: tomato mosaic, seedling inoculation.

Introduction

Broadbent (1965) established that the extent of internal TMV in tomato seeds depends upon the tomato cultivar, the time of infection in relation to flowering and fruit size and position on the plant. He also suggested possible variations with strains of the virus. Rast (1975) found only negligible amounts of TMV in the seed from plants inoculated in the seedling stage with the symptomless mutant MII-16 compared with those from plants inoculated with its parent tomato strain, isolate SPS.

Experiments are reported in this paper in which the extent of seed infection is investigated using other strains of TMV. Also seedling inoculation with MII-16 is used in an attempt to produce virus-free seed.

Material and methods

For the glasshouse experiments in 1975 and 1976 tomato plants cv. Moneydor (sown in January 2 in both years) were first grown in potting soil in plastic pots of 10 cm diameter and afterwards transplanted into plastic pails with a capacity of 10 l of soil. The plants were allowed to root through the perforated bottoms of the pails into another layer of 15–20 cm of potting soil on the benches of the glasshouse. This additional rooting substrate was a precaution against the physiological fruit disorder known as blossom end rot.

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For the experiment in which various strains were compared for the extent of seed infection in the first truss the plants were inoculated in the middle of February when the first truss was in flower. Earlier inoculation would have prevented truss development with some strains, particularly the tomato enation strain (isolate NH-69) and the yellow mosaic strain (isolate GPga). The other strains used were the tobacco strain (isolate MA), the tomato strain (isolate SPS), the yellow ringspot strain (isolate GdK), the winter necrosis strain (isolate SL^a), the crusty fruit strain (isolate MKv) and the symptomless mutant MII-16. The inoculum of each strain was prepared from purified suspensions stored in a deep-freeze at -18°C or from infected fresh leaves. All of the eight strains described by Rast (1975) were used in the experiment in 1975 and three of them in 1976.

Only TMV-free plants were used in the experiment and before inoculation they were all tested for the presence of TMV by sap inoculation of Nicotiana glutinosa even though they had all been grown from virus-free seed. For each of the eight strains batches of four plants were inoculated by dusting the terminal leaflets of 3-4 leaves per plant with 600 mesh carborundum and wiping them with a piece of cotton wool soaked in inoculum. In 1976 SPS was used to inoculate four extra plants from which all except the first trusses were removed when flowering. This treatment is indicated as SPS-b to distinguish it from the treatment without truss pruning SPS-a.

In 1975 and 1976 ripe fruits for seed extraction were harvested from the first truss from each plant separately. In 1976 after collecting fruits for the individual seed samples the fruits which were left to ripen on the first trusses in treatment SPS-b were bulked to give a composite seed sample. For MA, SPS-a and NH-69 bulk fruit samples were taken from the second trusses.

For studies of seed infection in a number of successive trusses plants were inoculated as seedlings about the middle of January with either MII-16 or SPS. Three categories of infected plants were distinguished. One category inoculated with SPS and showing normal tomato mosaic and two others inoculated with MII-16 and reacting either with or without symptoms which is indicated as MII-16⁺ and MII-16⁻ respectively. Of the plants infected with SPS four were used in 1975. Out of 30 plants inoculated with MII-16 five symptomless plants and five others showing mosaic symptoms were selected when the fifth truss was flowering. From each of the 14 plants five trusses were harvested separately for seed extraction. In 1976 five plants were used to represent SPS in the experiment. For each of the categories of plants infected with MII-16 two batches of five plants were selected when the first fruits ripened. Of a total of 25 plants seven trusses were investigated for seed infection, the fruits for each sample being collected from corresponding trusses from batches of five plants.

The seed pulp freshly extracted from a sample of fruits was first rinsed on a sieve in running tap water to get rid of the excess pulp and was then soaked for 1 h in 0.1 N HCl. After this treatment the sieve was used again to rub the seeds free from the surrounding gelatinous tissue which was eventually removed by repeated washings in ample quantities of tap water. For an additional external disinfection the air-dried seed samples were soaked for 15 min in a 10% solution of Na₃PQ₄ and then washed with tap water. After this treatment the seed samples were ready to be tested for the presence of internal TMV.

Ten sub-samples of 25 seeds each were tested from every sample. Each sub-sample was ground in a mortar with some fine, sterilized sand and 3 ml of water and then 224

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applied to three middle leaves on a *N. glutinosa* plant. A plug of cotton wool wrapped around a 6–8 cm bamboo pricker was used to apply the sample to the carborundum dusted leaves which were then rinsed with tap water. Lesions were counted after 3–4 days. As various factors may influence the susceptibility of test plants as many seed samples as possible were tested on plants of similar size within the shortest possible time. For the experiment with eight different strains of TMV all the seed samples were tested within a month on plants of three successive sowings.

A number of single lesions produced on N. glutinosa was transferred to a suitable host to establish whether the TMV strain isolated from the seed was similar to the one previously used to inoculate the tomato plant(s). Tobacco and tomato strains were differentiated on the 'necrotic' line of N. tabacum ev. White Burley or 'Dutch A' (Broadbent, 1962) which reacts with a systemic mosaic to the tobacco strain and with local necrotic lesions to tomato strains of TMV. The 'mosaic' line of N. tabacum ev. White Burley, a systemic host for TMV, was used to identify the yellow mosaic strain. The yellow ringspot strain was identified by the systemic symptoms produced on both N. tabacum cv. Samsun and N. glauca. The identity of the crusty fruit strain characterized by tiny local lesions on N. glutinosa was checked on tomato seedlings which react with necrotic dots along the veinlets of young unfolding leaves. Tomato seedlings were also used to identify the tomato enation strain which causes severe leaf malformations. No attempt was made to recover a symptomless strain from infected seed from plants inoculated with MII-16. In previous work (Rast, unpublished) it was established that infected seed of this source always contained a symptom-producing tomato strain, never a symptomless strain.

Heat treatment was investigated in an attempt to eliminate the small amounts of internal TMV from seed taken from MII-16 inoculated plants. For these experiments involving heat treatment the samples of tomato seed were placed in either open petri dishes or beakers and treated for 3 days in an oven at 76°C.

Results

The lesions counted on three leaves of a *N. glutinosa* plant for every sub-sample of 25 seeds tested were added and the total numbers of lesions obtained graded in an arbitrary manner (Fig. 1). In Figs. 2–6 the results obtained with the ten sub-samples of any one sample of seed have been arranged in a column.

The seed samples obtained from individual plants after inoculation with the tobacco strain MA show considerable variation in TMV content (Fig. 2). One sample has a moderate level of seeds infected while the three others have very low levels or are virus-free. For identification 42 lesions from *N. glutinosa* were transferred singly to plants of

Fig. 1. Legend to total numbers of local lesions counted on three leaves of a *Nicotiana glutinosa* plant after inoculation with sub-samples of 25 tomato seeds each.



Fig. 1. Legenda van de totale aantallen lokale vlekken geteld op drie bladeren van een Nicotiana glutinosa plant na inoculatie met deelmonsters van elk 25 tomatezaden.

Fig. 2. Internal TMV content of seed from batches of four plants infected with different strains of TMV when the first truss was in flower. Each column represents the test results obtained with a seed sample from all fruits of the first truss of one plant.

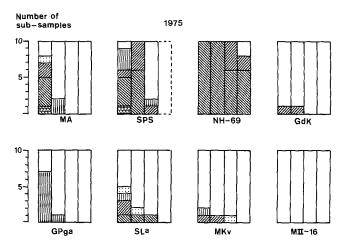


Fig. 2. Inwendig TMV-gehalte van zaad van groepen van vier planten geïnfecteerd met verschillende TMV stammen bij de bloei van de eerste tros. Elke kolom geeft de toetsingsresultaten weer van een zaadmonster van alle vruchten van de eerste tros van één plant.

Fig. 3. Internal TMV content of seed from batches of four plants infected with different strains of TMV when the first truss was in flower. Each column in the compound figures represents the test results obtained with a seed sample from fruits of the first truss of one plant. The separate columns stand for composite seed samples from fruits collected from either first (SPS-b) or second trusses (MA, SPS-a and NH-69) of four plants.

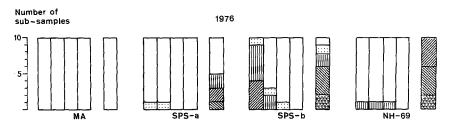


Fig. 3. Inwendig TMV-gehalte van zaad van groepen van vier planten geïnfecteerd met verschillende TMV stammen bij de bloei van de eerste tros. Elke kolom in de samengestelde figuren geeft de toetsingsresultaten weer van een zaadmonster van vruchten van de eerste tros van één plant. De afzonderlijke kolommen stellen samengestelde zaadmonsters voor van vruchten verzameld van eerste (SPS-b) of tweede trossen (MA, SPS-a en NH-69) van vier planten.

the 'necrotic' line of 'White Burley'. One lesion caused a systemic mosaic typical for the tobacco strain, whereas the other 41 induced local lesions typical for the tomato strain.

In 1976 the tobacco strain MA was passed through four cycles of selective multiplication on the 'necrotic' line of 'White Burley' using young systemically infected leaves as inoculum for each sub-culture. Precautions were taken to prevent the tomato strain

being introduced into the tomato plants after inoculation with the tobacco strain by separating them from the others by polythene screens, by handling them first and by using skimmed milk on hands. Seed produced by these plants remained free from TMV (Fig. 3).

Seed samples from plants infected with the tomato strain SPS showed varying proportions of TMV in seeds but because *Botrytis cinerea* caused premature ripening and abscission of fruits on one plant the data are incomplete (Fig. 2). All of the ten lesions isolated from *N. glutinosa* and transferred singly to the 'necrotic' line of 'White Burley' produced local lesions of the tomato strain.

The seed samples from the plants infected with the tomato enation strain are uniformly infected as compared with those obtained with SPS. Tests as individual seeds from four sub-samples of 25 seeds each showed that 2, 4, 8 and 2 seeds respectively were infected. The identity of NH-69 was confirmed by the severity of the leaf malformations developing on 20 tomato seedlings after inoculating each with a single lesion from *N. glutinosa*.

The differences in TMV content of the seed between SPS and NH-69 may have been related to the effects of the isolates on fruit set. SPS had no marked effect on fruit set so TMV could be distributed among all the fruits set whereas NH-69 caused a very poor setting resulting in few fruits and a concentration of the virus in the seed of these.

Pruning of trusses in treatment SPS-b induced a similar concentration of TMV in the remaining first trusses. Two out of four individual seed samples and the composite sample derived from this treatment contained more TMV than all other samples from first trusses obtained in the other treatments in 1976 (Fig. 3). Among the samples of SPS-b the composite sample showed the highest TMV content. With normal fruit set in treatments MA, SPS-a and NH-69 the amounts of TMV found in individual seed samples from the first trusses were too small to detect strain differences, but differences became apparent when composite seed samples from second trusses of fruits were tested (Fig. 3). Again the highest concentration was found with NH-69, although it did not affect fruit set as severely as usual.

Of the other strains used in 1975 only the winter necrosis strain SL^a caused an appreciable degree of seed infection (Fig. 2). Examination of lesions produced in the seed tests on *N. glutinosa* and transferred singly to *N. glauca* for identification showed that 37 of the 46 were typical of strain SL^a by producing local lesions, the other nine lesions giving no reaction on *N. glauca*.

With the yellow ringspot strain GdK only a small proportion of the seed samples was found infected by TMV. For strain identification the single lesions isolated from N. glutinosa were first cultured on N. tabacum cv. Samsun and then tested on N. glauca. Both host plants reacted with characteristic yellow ringspots to 19 out of the 20 isolates made. One isolate which produced a chlorotic mottle on Samsun did not visibly infect N. glauca.

With the yellow mosaic strain GPga the tests of the seed samples obtained from severely mottled fruits and containing many necrotic seeds indicated a low TMV content. All of the 15 lesions transferred singly from N. glutinosa to the 'mosaic' line of N. tabacum cv. White Burley for identification produced typical yellow mosaic symptoms.

With the crusty fruit strain MKv most of the fruits used for seed extraction were not affected by symptoms. The small number of infected seed samples induced small local

lesions on N. glutinosa characteristic for this strain. When transferred singly to tomato seedlings only two out of ten lesions produced symptoms of veinal necrosis, the other eight lesions giving an atypical mild mosaic. Fruits showing characteristic crusty fruit symptoms and collected from different trusses from plants previously used as a source of inoculum in this experiment contained no virus in the seed. This result was not included in Fig. 2.

In the experiment on seedling inoculation the seed samples show considerable differences in TMV content between similarly treated individual plants and between trusses (Fig. 4). However, the largest differences occur between the strains of TMV

Fig. 4. Internal TMV content of seed from plants infected as seedlings with either the tomato strain, isolate SPS, or its symptomless mutant, MII-16, with (+) or without (-) symptoms when the fifth truss was in flower. Each column represents the test results obtained with a seed sample from fruits of the indicated truss of one plant.

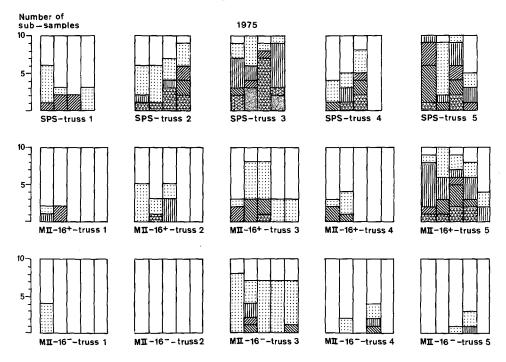


Fig. 4. Inwendig TMV-gehalte van zaad van planten als kiemplant geïnfecteerd met de tomate-stam, isolaat SPS, of de symptoomloze mutant MII-16, met(+) of zonder(-) symptomen bij de bloei van de vijfde tros. Elke kolom geeft de toetsingsresultaten weer van een zaadmonster van vruchten van de aangegeven tros van één plant.

used. With the tomato strain SPS all samples but the one from the 4th truss of the 4th plant contain TMV. The highest virus concentrations are also found with SPS. In the 1st plant a maximum is reached in seed from the 5th truss and in the 2nd, 3rd and 4th plant in seed from the 3rd truss.

With the symptomless mutant MII-16 a large proportion of the samples do not

Fig. 5. Internal TMV content of seed from plants infected as seedlings with either the tomato strain, isolate SPS, or its symptomless mutant MII-16, with (+) or without (-) symptoms when fruits of the first truss ripened. Each single or double column represents the test results obtained with (a) composite seed sample(s) from fruits of corresponding trusses of one or two batches of five plants respectively.

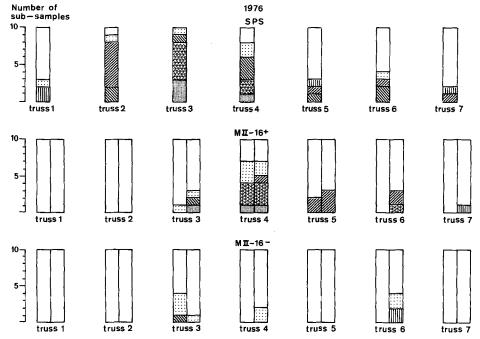


Fig. 5. Inwendig TMV-gehalte van zaad van planten als kiemplant geïnfecteerd met de tomatestam, isolaat SPS, of de symptoomloze mutant MII-16, met (+) of zonder (-) symptomen bij het rijpen van vruchten van de eerste tros. Elke enkele of dubbele kolom geeft de toetsingsresultaten weer van (een) samengesteld(e) zaadmonster(s) van vruchten van overeenkomstige trossen van respectievelijk één of twee groepen van vijf planten.

contain TMV or only in negligible amounts, especially from plants which remained symptomless. There is also a similar tendency as shown with SPS in the fluctuation of TMV concentrations with successive trusses. However, the plants which developed mosaic symptoms in spite of inoculation with MII-16 show a maximum seed infection in the 5th truss, and not in the 3rd truss as with SPS.

The variation in seed infection with individual plants is obscured by the use of the composite seed samples, but differences between the duplicate batches of plants inoculated with MII-16 are still apparent (Fig. 5). The left and right columns represent seed samples obtained from plants in inner and outer rows respectively in a gladshouse facing the south.

In 1976 the general pattern of distribution of TMV among the successive trusses is similar to that shown in Fig. 4. With the plants inoculated with SPS the maximum seed infection is again found in the 3rd truss. A similar trend is seen with the plants which remained symptomless after inoculation with MII-16, but those which developed symptoms show a marked increase in the incidence of TMV in seed from the 4th truss.

Fig. 6. The effect of heat treatment on internal TMV content of tomato seed. The double columns represent the test results obtained with seed samples of different origin either treated with Na₃PO₄ only (left columns) or also treated at 76 °C for 3 days (right columns). The top row refers to commercial samples each of a different cultivar. The middle row to a commercial sample of one cultivar tested four times. The bottom row is for composite samples deriving from the experiment with SPS and MII-16 in 1976 (see text).

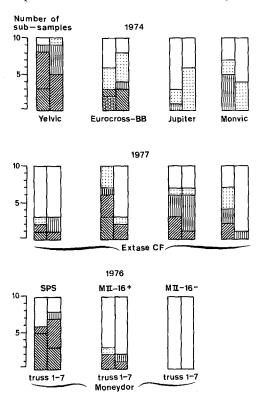


Fig. 6. Het gevolg van warmtebehandeling op het inwendig TMV-gehalte van tomatezaad. De dubbele kolommen geven de toetsingsresultaten weer van zaadmonsters van verschillende herkomst, alleen behandeld met Na_3PO_4 (linker kolommen) of tevens behandeld bij 76°C gedurende 3 dagen (rechter kolommen). De bovenste rij heeft betrekking op handelsmonsters elk van een verschillende cultivar. De middelste rij op een handelsmonster van één cultivar, dat vier maal werd getoetst. De onderste rij is voor samengestelde monsters afkomstig uit de proef met SPS en MII-16 (zie tekst).

Heat treatment for 3 days at 76°C in addition to a chemical treatment with Na₃PO₄ did not completely inactivate TMV in tomato seed but only lowered its TMV content as compared to the chemical treatment alone (Fig. 6). The TMV content may vary with commercial seed lots or even with samples taken from one lot. For heat treatment of the seed obtained in the experiment with SPS and MII-16 in 1976 (see Fig. 5) equal numbers of seeds were taken from each truss sample and mixed for each of the three categories of infected plants distinghuished. When the left parts of the double columns in the bottom row of Fig. 6 are compared to corresponding rows of single or double

columns in Fig. 5 it is obvious that this mixing resulted in a diluting effect on TMV concentrations. The TMV concentrations were further decreased by the heat treatment.

Discussion

The results presented in this paper show variation between the ability of different TMV strains to penetrate the seed during systemic infection of tomato plants. For instance, the tomato enation strain NH-69 and the tomato strain SPS are apparently more capable to do so than all other strains. The yellow mosaic strain GPga and the crusty fruit strain MKv which produce very marked symptoms in the plant result in a low content in the seed in spite of marked fruit symptoms. The tobacco strain MA and the symptomless mutant MII-16 could hardly be recovered from seed at all.

At present there is no explanation for the observed differences in TMV content of the seed. Some of the results suggest that when virus concentrations reached high levels elsewhere in the plant excess amounts of TMV occur in the seed. With the tomato strain SPS the seed from first trusses contained more TMV when all higher trusses had been removed than when left on the plant. The TMV content of individual and composite samples in treatment SPS-b suggested that the proportion of infected seeds in the fruits increased from the proximal to the distal ends of the first trusses. However, while with SPS the pruning of trusses had an unmistakable concentrating effect the reverse was not observed with the enation strain NH-69. The almost normal fruit setting in 1976 would be expected to reduce the incidence of seed infection but compared to SPS-a the largest number of infected seed samples was again found with NH-69. In former experiments (Rast, unpublished) the tobacco, tomato and enation strains were found to reach similarly high concentrations in tomato foliage giving dilution end points of between 10⁻⁶ and 10⁻⁷ for each of these strains. With the yellow mosaic and yellow ringspot strains the dilution end points were 10^{-4} and 10^{-5} respectively. These values would fit in with the present results if the high concentrations of the tobacco strain in leaf sap had not been contrary to its near absence in seed. It is therefore unlikely that differences in the extent of seed infection between strains are simply a matter of virus concentration.

The presence of tomato strain TMV in seed from plants inoculated with the tobacco strain MA may have resulted from the inability of the tobacco strain to interfere with the tomato strain. In former work (Rast, 1975) the tobacco strain was shown to be a poor competitor in tomato and could be replaced by the tomato strain even when the latter was introduced later. This probably happened by accident during the experiment in 1975.

The symptomless mutant MII-16 has been shown to interfere with the multiplication of other tomato strains (Rast, 1975). With the possible exception of the samples from the fifth and fourth trusses in 1975 and 1976 respectively the seed from plants inoculated as seedlings with MII-16 consistently contained less TMV than seed from plants inoculated with SPS. MII-16 is mostly contaminated by a symptom producing strain with a faster rate of multiplication and possibly identical to the parent strain SPS. By the initial predominance of the symptomless mutant tomato strain TMV is nevertheless prevented from infecting seed of at least one or two of the lowermost trusses. In this respect seedling inoculation with MII-16 is similar to a late infection

with tomato strain TMV. With plants inoculated when flowering in the fifth truss Broadbent (1965) did not find internal TMV in the seed from first and second trusses or found only small amounts of it. Following seedling inoculation with MII-16 the final extent of seed infection undoubtedly depends on the purity of the mutant in the inoculum and on the susceptibility of the individual plants which may or may not react with symptoms. The similarity in the distribution pattern of TMV among seed of successive trusses furthermore suggest external factors acting alike on the physiological condition of the three distinguished categories of infected plants.

The fluctuations in TMV content should be taken into account when considering the use of MII-16 in seed production. The results show that even a symptomless plant does not always produce virus-free seed. It would be wise to include regular testing of the seed with every extracted lot of seed from plants inoculated with MII-16.

Heat treatment will not adequately reduce the TMV content of seed samples with moderate to high TMV concentrations. However, it may be useful to eliminate TMV from seed samples with low virus concentrations like those obtained from plants remaining symptomless after inoculation with MII-16.

In summary it may be concluded that MII-16 may be successfully used to increase the production of comparatively virus-free seed if only infected but symptomless plants are used. However, such a practice must be accompanied by a regular check of the TMV content of the seed and heat treatment used when necessary.

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Samenvatting

Infectie van tomatezaad door verschillende stammen van tabaksmozaïekvirus, in het bijzonder met betrekking tot de symptoomloze mutant MII-16

Acht in symptoomexpressie verschillende stammen van het tabaksmozaïekvirus (TMV) vertoonden na inoculatie van tomateplanten bij de bloei van de eerste tros verschillen in de hoeveelheden TMV die in het zaad van de eerste tros werden gevonden (Fig. 2). Het hoogste TMV-gehalte werd gevonden voor de enatiestam, isolaat NH-69. Voor de tomatestam, isolaat SPS, en de winter-necrosestam, isolaat SL^a, werd een matig TMV-gehalte van het zaad vastgesteld. De gele kringvlekkenstam, isolaat GdK, de geelmozaïekstam, isolaat GPga, en de vruchtkorstenstam, isolaat MKv, veroorzaakten een laag TMV-gehalte. De tabaksstam, isolaat MA, en de symptoomloze mutant MII-16 bleken niet of nauwelijks tot zaadinfectie in staat.

De verschillen tussen de enatie-, tomate- en tabaksstammen werden in een tweede proef bevestigd (Fig. 3). Hierbij kon het TMV-gehalte van het zaad van planten, die geïnoculeerd waren met de tomatestam, verhoogd worden door de toepassing van trossnoei (zie SPS-b in Fig. 3).

Vergeleken met de tomatestam gaf de symptoomloze mutant MII-16 na inoculatie van tomateplanten in het kiemplantstadium steeds aanleiding tot een lager TMV-

gehalte van het zaad van een aantal opeenvolgende trossen (Fig. 4 en 5). Vooral het zaad van planten, die lange tijd na de inoculatie met MII-16 symptoomloos waren gebleven, bevatte betrekkelijk weinig of geen TMV. Het uit dergelijk zaad geïsoleerde virus behoort tot de tomatestam van het TMV, die als verontreiniging in het inoculum van MII-16 voorkomt en uiteindelijk mozaïeksymptomen veroorzaakt.

Een droge warmtebehandeling gedurende drie dagen bij 76°C bleek het TMV in zaad met een matig tot hoog TMV-gehalte niet geheel te inactiveren (Fig. 6). De handeling zou echter gebruikt kunnen worden als aanvulling op het gebruik van MII-16 voor een opzettelijke kiemplantbesmetting ter verkrijging van virusvrij zaad.

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Book review

P. R. Scott and A. Bainbridge (Eds), 1978. Plant disease epidemiology. 305 pp. of text, including tables and illustrations, references at the end of each contribution, and 23 pp. of subject index; bound. Blackwell Scientific Publications, Oxford, London, Edinburgh, Melbourne. Price £ 9.

After World War II two field-oriented subdisciplines of plant pathology flourished: chemical control and epidemiology. Nowadays there is general concern about the bio-hazards and high costs of chemical control, especially as it often gives only temporary relief. There is an obvious need for control of chemical control. Fortunately, epidemiology also prospered, at least for fungal diseases, and achievements in this area are now being applied to limit the use of chemicals in two ways. Firstly, by providing the knowledge necessary for forecasting epidemics and thus enabling growers to tailor their control measures and, secondly, by giving a theoretical basis for a wise use of the available sources of genetic resistance in plants. This very practical goal of plant disease epidemiology and many other aspects of this branch can be found in the present book, which is a collection of selected papers presented at the conference on Plant Disease Epidemiology and Dispersal of Plant Parasites, organized by the Federation of British Plant Pathologists in London, December 1977.

The book contains a variety of review articles, case studies of various diseases, and descriptions of specific techniques. The 33 regular papers are arranged in five sections, each section beginning with an additional comment from the chairman.