

YIELD OF GLASSHOUSE TOMATOES AS AFFECTED BY STRAINS OF TOBACCO MOSAIC VIRUS¹

*De invloed van stammen van het tabaksmozaïekvirus op de
opbrengst van kastomaten*

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In the latter part of the summers of 1963, 1964 and 1965 the effect of an early inoculation with different strains of tobacco mosaic virus (TMV) upon yield was investigated. All experiments were carried out in the same glasshouse-compartment and with the tomato variety 'Moneymaker', the plants being grown in plastic pails containing ordinary potting soil. In 1963 a green strain, a distorting strain and a yellow (or aucuba) strain were used, all capable of causing local lesions on *Nicotiana tabacum* 'White Burley', which reaction is characteristic for the tomato-type of TMV. Since unfavorable conditions affected control plants more than infected plants, the green strain caused no significant loss of yield. Plants infected by this strain yielded only 3% less weight of fruit than the control plants and even had a 12% greater number of fruits. Plants infected by either the distorting or the yellow strain yielded 43 and 65% respectively less weight of fruit and 32 and 48% respectively fewer fruits. In 1964 the same green strain of the tomato-type TMV was compared with a green strain of the tobacco-type TMV, which is characterized by a systemic reaction on 'White Burley'. Plants infected by the tomato-type and tobacco-type green strains yielded 16 and 21% respectively less weight of fruit than the control plants and 11 and 18% respectively fewer fruits. In 1965 the same green strain of the tomato-type TMV was used and compared with another green strain of the same virus, which in addition caused local lesions on *N. glauca*, and with a yellow ringspot strain, which showed the tomato-type reaction on 'White-Burley'. Plants infected with these three strains yielded 14, 18 and 17% respectively less weight of fruit than the control plants, but only 2, 6 and 6% respectively fewer fruits. The relatively small reduction in the number of fruits and an appreciable delay of the harvest probably resulted from the fact that the plants in this experiment were inoculated in the seedling stage.

INTRODUCTION

Data on the effect of different strains of TMV on the yield of tomatoes are relatively scarce. MESSIAEN & MAISON (1962) published data on differences in yield obtained with a common strain and an aucuba strain. MCRITCHIE & ALEXANDER (1957) ascribed differences in the degree of yield depression obtained in two successive years with the same susceptible tomato varieties to a pathogenic difference between the TMV-isolates used. This was evidenced by the fact that a tolerant hybrid which remained symptomless in the first year showed mosaic symptoms in the next year. In yield experiments concerned with time of infection BROADBENT (1964a) compared different isolates of the common green strain, but did not observe differences in yield. An experiment in which HOLMES's "masked strain" was used unfortunately did not allow comparisons to be made because of its failure to protect the plants against super-

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infection by the common green strain, which served as the standard-treatment. SELMAN (1941) made a detailed study of the effects of JOHNSON's tobacco virus no. 1 and two strains of tomato mosaic virus on yield and quality of tomatoes.

It seemed worthwhile to make a further contribution towards this practical aspect of the knowledge of TMV-strains. This paper presents the results of three years' experiments designed to study the effects of six symptomatologically different strains on the yield of tomatoes.

MATERIALS AND METHODS

The experiments were carried out in the latter part of the summers of 1963, 1964 and 1965 in the same glasshouse-compartment. The tomato variety 'Moneymaker' was used each year as test plant. The young plants were raised first in small plastic pots and transplanted afterwards to plastic pails with a capacity of six litres. These pails were perforated at the bottom and were placed upon rubber dishes with a diameter of 30 cm and a depth of 6 cm. The plants were grown in ordinary tomato potting-soil which received an additional dressing of fertilizer in 1964 and 1965, but not in 1963. When the experiments started in 1963 it was thought that watering could best be done by trickle-irrigation. This, however, proved a failure. It appeared that healthy plants need more water than infected plants; thus the former were often dry when some of the latter were still flooded. Since it was not possible to provide a separate manipulation-device for each treatment, this method of watering was replaced by hand-watering. Water was given two or three times a week on top of the soil in 1963 and into the rubber dishes in 1964 and 1965.

For these experiments the glasshouse-compartment was subdivided into sixteen blocks for eight plants each. This plan allowed for four treatments to be replicated four times so making up thirty-two plants per treatment. The replications were distributed according to a randomized block design. The treatments consisted of one or two non-inoculated controls and infection either with three or two TMV-strains respectively. The inocula were prepared by grinding infected leaf-material with mortar and pestle, with addition of tap-water, and were then applied to the carborundum-dusted leaf-surface with a piece of cotton. The developmental stage of the plants at the time of inoculation differed slightly in the successive years. In 1963 and 1964 the plants had fully developed their third and fourth leaves respectively, whereas in 1965 the plants were still in the cotyledon-stage when inoculated.

Much care was taken to prevent TMV-infection of the control plants. The plastic pails were soaked in a solution of soap and trisodium-phosphate for 24 hours and then thoroughly scrubbed and rinsed with tap-water before use. The potting-soil was steam-sterilized only a few days before transplanting. The surface of the glasshouse-soil was entirely covered with polythene sheets in 1963. Since this procedure tended to create an excessively dry atmosphere the soil-surface after steam-sterilization was only partially covered in 1964, the path being left open. In 1965 steam-sterilization only was applied.

To prevent contact between plants in adjacent blocks these were separated by polythene screens two metres square. During cultural operations a white overall, changed every week, and a pair of rubber boots, scrubbed with soap before entering the trial, were worn. Control plants were handled first, a pair of poly-

these gloves being used only once for a single row of four plants. Visitors were excluded from the trial, the glasshouse-compartment being kept locked during most of the time. Despite these and other measures some of the control plants became infected as was shown by regular assays on *Nicotiana glutinosa* or *N. tabacum* 'Xanthi nc', young side-shoots of every second or third pruning-round usually being used for this purpose. The first assay was made a week before transplanting, the last one about the time when the first fruit ripened. When harvest started preventive measures were dropped for lack of time as the fruits of the lowermost four trusses were picked and weighed individually.

The single-lesion isolates used in the experiments were derived from TMV-strains which differed in their symptoms on a number of test plants. The abbreviations used to indicate them in this paper refer to symptoms and source of the original tomato leaf-sample with the exception of A.29, which stands for ALEXANDER'S isolation no. 29 (cf. ALEXANDER, 1962).

- Isolate A.29 was derived from a green strain of the tobacco-type of TMV, which caused a systemic reaction on 'White Burley'.
- Isolate SP was derived from a streak-diseased tomato plant. It represented a green strain of the tomato-type of TMV since it caused only local lesions on 'White Burley'. This local reaction was also shown by the other isolates.
- Isolate SL represented another green strain which, however, was furthermore characterized by its ability to cause local necrotic lesions on *N. glauca*. In this respect it resembled the TMV-strain for which the name *Marmor tabaci* Holmes var. *siccans* was proposed by DOOLITTLE & BEECHER (1942). SL was also isolated from a streak-diseased tomato plant.
- Isolate NP was isolated from a plant showing leaf-narrowing and represented a distorting strain. It was characterized by the development of enations on the lower sides of tomato leaves and agreed fully with the description of the tomato enation strain (AINSWORTH, 1937) or the tobacco distorting virus (SMITH, 1957: 518-519).
- Isolate GP was isolated from a leaf-sample showing yellow mosaic and represented a yellow strain probably identical with tomato aucuba virus (SMITH, 1957: 520).
- Isolate GK was isolated from a yellow ringspot on a tomato leaf and was the subject for the description of the tomato yellow ringspot strain (RAST, 1965a).

Sowing, planting and harvesting dates are shown in Table 1.

TABLE 1. Relation between sowing-date, planting-date and harvest-period.
Verband tussen zaaidatum, plantdatum en oogstperiode.

Year	Sowing date	Planting date	Harvest period
1963	5 June	17 July	13 Sept.- 6 Nov.
1964	12 June	23 July	2 Oct. -24 Nov.
1965	21 June	30 July	20 Sept.- 2 Nov.

RESULTS

As already stated, the measures taken to prevent infection of the control plants did not completely do so. In 1963 twelve out of thirty-two plants became infected according to the assays made before harvest. As a matter of fact this hardly affected the results of the statistical analyses and so these infected control plants have been included in the figures. Likewise in 1965, when eight out of thirty-two plants became infected, all of them were taken into account. In 1964, however, when the experiment was started with the double number of control plants plus eight reserve plants, sixteen of seventy-two plants were discarded as soon as infection was detected by assay. The results of three years' yield experiments have been compiled in Table 2, which is based on a minimum fruit weight of 25 gram.

TABLE 2. Fruit yield of four trusses based on fruits heavier than 25 g.
Vruchtopbrengst van vier trossen op basis van vruchten zwaarder dan 25 g.

Year	Treatment	Yield of fruit per plant				Average	
		Weight		Number		fruit weight	
		g	%		%	g	%
1963	Control	801	100	13.0	100	61.4	100
	SP	787	97.0	14.6	112.3	53.8	87.6
	NP	460	56.8	8.9	68.4	51.7	84.2
	GP	280	34.6	6.8	52.3	40.8	66.4
1964	Control	1.247	100	21.7	100	57.3	100
	SP	1.044	83.7	19.4	89.4	53.9	94.0
	A.29	989	79.3	17.8	82.0	55.3	96.5
1965	Control	1.356	100	19.3	100	70.3	100
	SP	1.168	86.1	19.0	98.4	61.3	87.2
	SL	1.107	81.6	18.1	93.7	61.8	87.9
	GK	1.119	82.5	18.2	94.3	61.1	86.9

In 1963 the difference between the yield of control plants and that of plants infected with SP was not significant. However, the differences between the control treatment and SP on the one hand and NP and GP on the other hand were highly significant ($P > 0.01$). The difference in weight of fruits found between NP and GP was also significant ($0.05 > P > 0.01$), though the difference in number of fruits was not ($0.1 > P > 0.05$). As regards the average fruit weight, the differences between treatments were all highly significant except for that between SP and NP.

In 1964 the differences in yield between the control treatment and both SP and A.29 were highly significant; those between SP and A.29 were not significant, although the difference in number of fruits was nearly so ($P = 0.1$). No significant differences were observed in the average fruit weights.

In 1965 there was a highly significant difference in weight of fruits between the control treatment on the one hand and SP, SL and GK on the other hand, though none between SP, SL and GK themselves. Since no significant differences were found between treatments with regard to the number of fruits, the

differences in average fruit weight were again highly significant between control and other treatments.

The procedure of picking and weighing the fruits individually was adopted in 1963 to ascertain whether or not the observation was correct that control plants yielded heavier fruits. The routine of collecting also the non-set fruits was prompted by the considerably greater proportion of these among the produce of the NP-treatment and furthermore furnished another measure for the fruit-set in general. Both fruits and non-set fruits were graded into weight-classes for which boundaries were set at 25, 50, 75 and 100 gram (grades IV, III, II and I). The distribution of the numbers of fruits according to this weight classification is presented in percentages for each treatment in Fig. 1. It will be seen that in 1963 the control treatment yielded more heavy fruits in grades I and II than did isolate SP. The effect of NP on the formation of non-set fruits (grade V) is striking and reminds one of the action of certain growth hormones in inducing parthenocarp. In 1964, when no significant differences were found in the average fruit weight between treatments, the same tendency towards heavier fruits in the control treatment was reflected only in a slightly greater proportion of fruits in grades I and II. In 1965 the control treatment yielded a considerably higher number of fruits in grade I and a smaller number of fruits in grade III as compared with the other treatments, and together these account for the highly significant difference in the average fruit weight.

In order to ascertain whether or not infection with the different TMV-strains had caused a delay in the harvest a mean harvest date was calculated for each treatment. This was done as follows: The yield at every picking date was

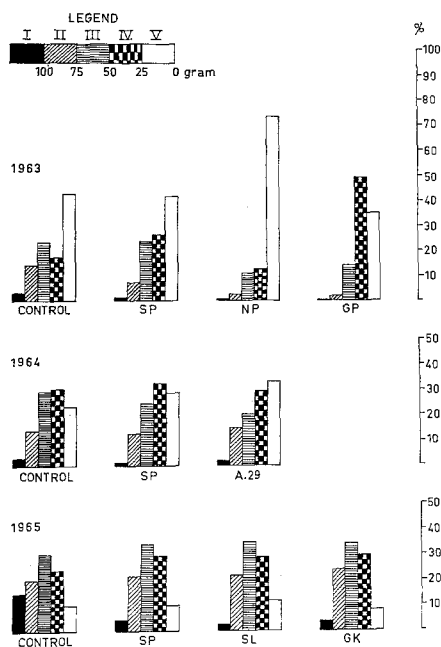


FIG. 1.

The distribution of numbers of fruit according to weight-classes in per cent per treatment. The TMV-isolates A.29, SP, SL, NP, GP and GK represent a green strain of the tobacco type of TMV, two green strains of the tomato type of TMV, a distorting strain, a yellow strain and a yellow ringspot strain respectively.

De verdeling van de aantallen vruchten volgens gewichtsklassen in procenten per behandeling. De TMV-isolaties A.29, SP, SL, NP, GP en GK vertegenwoordigen respectievelijk een groene stam van het tabakstype TMV, twee groene stammen van het tomaattype TMV, een misvormende stam, een gele stam en een gele-kringvlekkenstam.

TABLE 3. Delay of harvest by TMV-infection.
Oogstverlating door TMV-infectie.

Year	Treatment	Mean harvest date	
		Number of days after first picking	Approximate calendar date
1963	Control	31.8	15 Oct.
	SP	28.4	21 Oct.
	NP	33.9	17 Oct.
	GP	37.6	20 Oct.
1964	Control	26.7	29 Oct.
	SP	26.0	28 Oct.
	A.29	24.5	27 Oct.
1965	Control	17.8	8 Oct.
	SP	28.4	18 Oct.
	SL	27.5	18 Oct.
	GK	29.6	20 Oct.

multiplied by the number of days elapsed since the first picking date. The sum of the products was then divided by the sum of the yields. The mean harvest dates thus obtained are presented in Table 3, together with the approximate calendar dates.

In 1963 isolates GP and SP caused a delay in harvest date of five and six days respectively. The two days' difference between the control treatment and NP was not significant and in fact the first ripe fruits were picked from NP-infected plants. In 1964 no apparent delay in harvest date could be observed, whereas in 1965 infection caused a minimum delay of ten days. Mean harvest dates have been marked on the cumulative graphs of Fig. 2 representing the actual course of the harvest.

No marked defects in quality were observed on the fruits throughout the years, except that GP caused yellow angular spots on nearly all fruits, rendering them totally worthless. From this point of view the commercial loss of yield caused by this particular strain would amount to the full 100%. NP occasionally caused a slight elongation of the mature fruits, but the instances in which this occurred were few and were not taken into consideration.

DISCUSSION

Although the experiments were carried out under similar conditions they can hardly be compared with each other. At best it can be stated that the increasing yields reflect the author's progress in the art of growing tomatoes.

In 1963 the control plants suffered most from the dry atmosphere created by sealing off the soil surface with polythene sheets and by insufficient watering. The harmful effects of drought upon fruit set were probably aggravated by nitrogen deficiency towards the end of the growing period. All this tended to depress the yield of the control plants to such an extent that it almost eliminated any difference between these and SP-infected plants that no doubt would have developed with more adequate cultural methods.

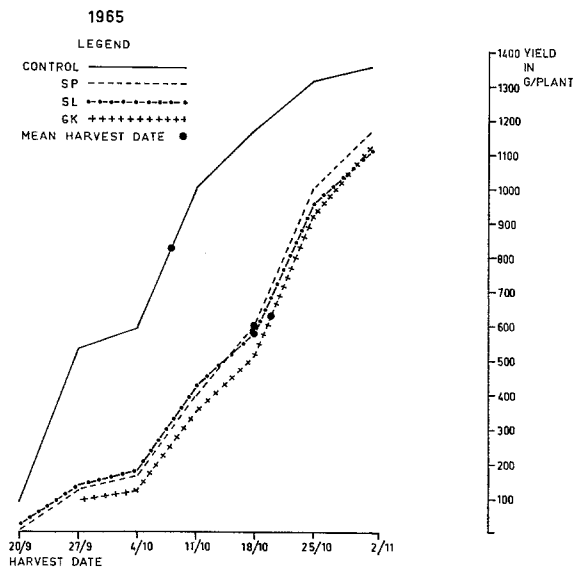
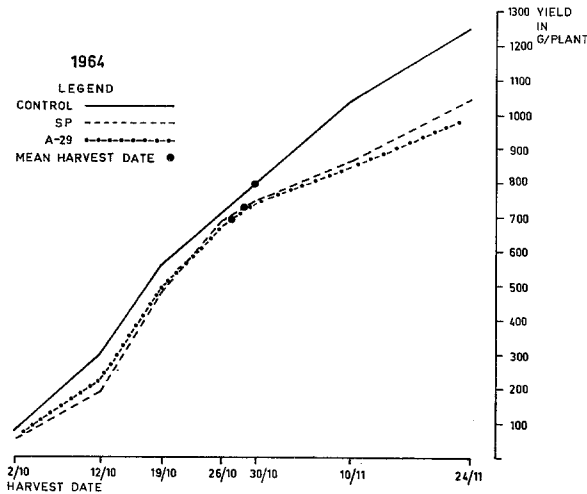
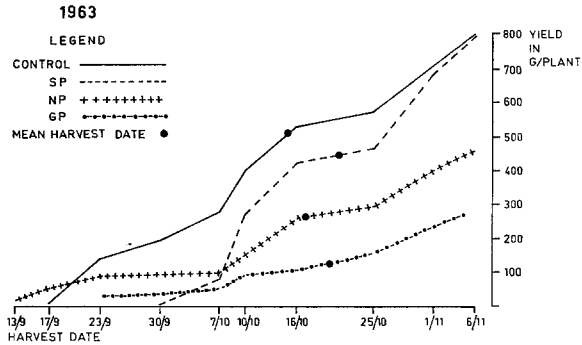


FIG. 2. Cumulative graph of the actual course of the harvest. The TMV isolates A.29, SP, SL, NP, GP and GK represent a green strain of the tobacco type of TMV, two green strains of the tomato type of TMV, a distorting strain, a yellow strain and a yellow ringspot strain respectively.

Cumulative grafiek van het werkelijke verloop van de oogst. De TMV-isolates A.29, SP, SL, NP, GP en GK vertegenwoordigen respectievelijk een groene stam van het tabakstype TMV, twee groene stammen van het tomaattype TMV, een misvormende stam, een gele stam en een gele-kringsplekkenstam.

The plants infected with NP or GP did not seem to be affected so much by the adverse cultural conditions referred to above. It would therefore be expected that the differences from the control treatment would have been more pronounced if these conditions had not prevailed. Nevertheless the loss of yield caused by infection with NP is considerable. As far as is known from the literature, truly distorting strains like NP have not yet been used in yield experiments.

SELMAN (1941), working with strains A.15 and A.17 of the tomato mosaic virus, discussed the formation of enations, which apparently were connected with renewed active growth after a period of sustained watering. However, because of the temporary nature of these enations A.15 and A.17 were not considered identical with AINSWORTH's tomato enation strain (1937) for which enations are a permanent feature, as is also the case with NP.

The isolate used in the present experiment answers AINSWORTH's description in all other respects e.g. when mention is made (SMITH, 1957: 519) of the conical shape of the fruits. This malformation could be observed especially with the non-set fruits and together with their excessive production reinforces the picture of NP acting like a growth hormone.

That a severe yellow strain like GP should cause the heaviest loss of yield was fully expected since one of the observed effects of the infection consisted of the abscission of many flower buds. The yield reduction determined is of the same order of magnitude as that reported by MESSIAEN & MAISON (1962) for LIMASSET's aucuba strain, which caused a 50% loss of weight in field-grown tomatoes.

In 1964, infection with SP and A.29 depressed yields, relative to the control treatment, to the same extent, since no statistical significance could be attached to the small differences obtained. This result was not altogether surprising since it confirmed the results of a pilot experiment in the open soil which indicated that A.29 had only a slightly more depressive effect on yield than SP. Another experiment, following the one under discussion, again showed the same tendency (RAST, 1956b). In this connection it is noted that SELMAN (1941), also, found no appreciable differences between the effects of A.15 and A.17, which are described as two strains of the tomato mosaic virus, and JOHNSON's strain of tobacco mosaic virus, the yield depressions by weight being 15, 22 and 20% respectively.

In 1965 the most interesting result was the relatively small effect of infection upon the number of fruits. In commercial tomato growing it is a common experience that fruit-set on one or two flower trusses is impaired following TMV-infection. This observation has been more or less confirmed by various experiments on the effect of time of infection, early inoculation almost invariably having a more severe effect on the number of fruits harvested than late inoculation (BROADBENT, 1964a; BERGMAN & BOYLE, 1965). It should be pointed out, however, that early inoculation in most of the experiments reported in the literature has been performed about the time of flowering of the first truss, and this has badly affected the fruit-set on higher trusses. Late inoculation, on the other hand, has often taken place at a moment when the number of trusses required for the observations intended (e.g. fruit quality effects) had already set fruit and consequently has figured better in the results.

In this connection reference should be made to studies concerning the de-

siccative effects of TMV-infection upon the vital flower parts, made by the section of Plant Physiology of the Horticultural Experiment and Research Station at Naaldwijk. The salient points emerging from these studies were that the desiccation affected both the stigmas and the pollen, impairing the stickiness of the stigmas and the germination of the pollen, and that these effects could be observed to last for six weeks following inoculation. Non-inoculated plants and plants inoculated in the seedling stage produced pollen of a consistently better quality than plants inoculated when the first truss became visible, the pollen of the latter showing a sharp drop in percentage germination around the fourth week after inoculation (VAN RAVENSTEIN, 1965).

On the basis of these results it appears justified to ascribe the nearly equal numbers of fruits in the experiment of 1965 to the inoculation having been performed in the seedling stage, which is a long time ahead of the flowering stage.

Furthermore it is remarkable that no differences were obtained between infections with SP and SL, representing green strains, on the one hand, and GK, as a representative of the yellow ringspot strain, on the other hand. This result is difficult to explain, since it seemed logical to expect that GK, because of its more severe leaf symptoms and being a distinctive yellow mosaic, would depress yields more than SP or SL.

The delay in harvest resulting from TMV-infection, which is most pronounced in this experiment, is presumably also due to the very early inoculation. In this connection reference is made to BROADBENT (1964b) who, discussing the prospects of a deliberate seedling inoculation as a means of avoiding yield and quality losses, recommends a two to three weeks' advance in sowing date in order to be commercially acceptable.

From the overall results of the present experiments it is concluded that unfavorable conditions may affect non-inoculated plants more than infected ones, thereby creating the danger of interpreting the absence of differences in yield in terms of mildness of the strain used. When the plants are better cared for, higher yields are obtained from non-inoculated plants as compared with infected plants. Apart from the distorting and severe yellow strains, only minor differences in yield depression were obtained with the TMV-strains used in these experiments, despite distinctive symptomatological differences.

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SAMENVATTING

In 1963, 1964 en 1965 werd in de nazomer het effect van een vroege inoculatie met verschillende stammen van het tabaksmozaïekvirus (TMV) op de opbrengst van tomaat nagegaan. Alle proeven werden uitgevoerd in dezelfde kas en met het tomateras 'Moneymaker'; de planten werden opgekweekt in plastic emmers die met gewone potgrond gevuld waren.

In 1963 werden een groene stam, een misvormende stam en een gele (of aucuba-)stam gebruikt, welke alle in staat zijn de voor het tomaattype TMV karakteristieke lokale lesies te veroorzaken op *Nicotiana tabacum* 'White Burley'. Aangezien ongunstige omstandigheden de controleplanten nadeliger beïnvloedden dan de geïnfecteerde planten, veroorzaakte de groene stam geen duidelijk opbrengstverlies. Planten, die met deze stam geïnfecteerd waren, brachten slechts 3% minder aan vruchtgewicht op dan de controleplanten en zelfs 12% meer vruchten. Planten, geïnfecteerd met de misvormende of met de gele stam, brachten respectievelijk 43 en 65% minder aan vruchtgewicht op en respectievelijk 32 en 48% minder vruchten.

In 1964 werd dezelfde groene stam van het tomaattype vergeleken met een groene stam van het tabakstype TMV, welke gekarakteriseerd wordt door een systemische reactie op 'White Burley'. Planten, geïnfecteerd met de groene stam van het tomaattype of tabakstype TMV, brachten respectievelijk 16 en 21% minder aan vruchtgewicht op dan de controleplanten en respectievelijk 11 en 18% minder vruchten.

In 1965 werd opnieuw dezelfde groene stam van het tomaattype TMV gebruikt en vergeleken met een andere groene stam van hetzelfde virus, welke bovendien lokale necrotische lesies veroorzaakt op *N. glauca*, en met een gelekringvlekkenstam, welke eveneens de tomaattype-reactie vertoont op 'White Burley'.

Planten, welke met een van deze stammen waren geïnfecteerd, brachten respectievelijk 14, 18 en 17% minder aan vruchtgewicht op dan de controleplanten, maar slechts 2, 6 en 6% minder vruchten. De betrekkelijk geringe reductie in het aantal vruchten en een aanzienlijke oogstverlating waren waarschijnlijk het gevolg van het feit dat de planten in deze proef in het kiemplantstadium waren geïnoculeerd.

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