Neth. J. Pl. Path. 81(1975) 205–216

Variability of some plant species from different origins and their suitability for virus work[1]

J. P. H. VAN DER WANT, M. L. BOERJAN and D. PETERS

Laboratory of Virology, Agricultural University, Wageningen, the Netherlands

Accepted 22 May 1975

Abstract

Plants of four species obtained from various sources were raised and compared for their suitability as test plants for a number of viruses. The species comprised *Chenopodium amaranticolor* (local lesion host of red clover mottle virus), *Nicotiana glutinosa* (local lesion host of tobacco mosaic virus (TMV)), *N. rustica* (systemic host of TMV, cucumber mosaic virus and tomato spotted wilt virus) and *N. tabacum* 'White Burley' (systemic host of TMV).

Some sources proved to be more attractive as test plants or experimental hosts because of, e.g., production of more local lesions per unit of leaf area (*C. amaranticolor* and *N. glutinosa*), distinctness of lesions (*C. amaranticolor*), development of more pronounced systemic symptoms (*N. rustica* and *N. tabacum* 'White Burley'), better growth characteristics (particularly *C. amaranticolor* and *N. rustica*), smoother leaves being easier to rub (*N. glutinosa*) or more and bigger leaf formation (particularly *N. rustica*).

The implications for the interpretation of host range studies and the quest for propagation and assays hosts are discussed.

Introduction

Nowadays, viruses are characterized by various physical, chemical and serological techniques. This has greatly enlarged the understanding of the similarities and differences between viruses and has enabled us to compare different virus isolates. As viruses are biological entities possessing the power to infect susceptible organisms, studies involving the inoculation of suitable plants remain necessary for providing additional information about different virus isolates. The symptoms produced by a virus on various plant species and cultivars may be an even more sensitive means of differentiating between isolates (McRitchie and Alexander, 1963) than any physical, chemical and serological technique (Mosch et al., 1974). Only part of the virus genome is expressed in properties which can be studied by these techniques. In order to be able to compare the work on the biological properties of viruses from different laboratories it is necessary that the plants of any species or cultivar used are genetically identical. Bos (1967), in his discussion about the problems of test plant variability, has already pointed to the fact that different selections of certain host plants, or any one species from different origins may differ in their response to certain viruses. Demski (1968) found large differences in the response of *Chenopodium album* from different sources to watermelon mosaic virus. The need for internationally accepted standardi-

[1] This article is an extended version of a paper presented by the same authors at the 2nd. International Congress of Plant Pathology, September 5–12, 1973.

zation of test plants has been advocated by various authors. Bos et al. (1960) emphasised the need for exchange of seeds of test plant species and cultivars between plant virologists.

It is now generally realized that related cultivars can differ considerably in their capacity and suitability to act as indicators in diagnostic studies, as local lesion hosts for quantitative virus assay or for the propagation of viruses in the laboratory. Consequently most publications dealing with plant viruses mention cultivar names of the plant species used.

Nevertheless, doubt may be raised as to whether such cultivated plants presented under a certain name are always genetically identical to those used by others with the same cultivar name. This may not necessarily be a matter of misnomer. Most, if not all, cultivars have been selected for their agronomic value and not for virological features. Thus a cultivar may be morphologically uniform but this does not imply uniformity and stability of its reaction to viruses, as shown by Kassanis and Selman (1947) for 'White Burely' tobacco and different strains of tobacco mosaic virus.

When wild species are being used for plant virus work, despite Demski's report, it is generally not recognized that samples from different sources may differ as widely in genetical make-up as different cultivars of a certain crop, and consequently may differ considerably in susceptibility and/or sensitivity to virus infection. Moreover there may be differences in growth characteristics, size and shape of leaves, etc. making one source more appropriate for virus studies than another. Only in a few rare instances, an effort has been made to select plants with special qualities for virus work, e.g. the East Malling clone of *Fragaria vesca* (Harris and King, 1942); the EMK clone of *F. vesca* (Fulton, 1960); the UC4, UC5 and UC6 clones of *F. vesca*, and the UC10, UC11 and UC12 clones of *F. virginiana* (Frazier, 1974). Köhler (1953) selected the *Solanum demissum* hybrid A6 for work with potato viruses.

Although some work has already been done, we felt a need to study further the occurrence of differences in the sensitivity and susceptibility present in sources of plant species commonly used for virus work and whether other characters important in virus research also varied. The present paper deals with our experiences with *Chenopodium amaranticolor*, *Nicotiana glutinosa*, *N. rustica;* and *N. tabacum* 'White Burley'.

Materials and methods

Many virologists kindly provided lots of seed samples on request. Experiments were conducted with 16 sources of *C. amaranticolor*, 17 of *N. glutinosa*, 13 of *N. rustica*, and 17 of *N. tabacum* 'White Burley'.

Plants were grown from seed according to the method routinely used in our laboratory. Seeds were sown in pans filled with soil mixture (Trio, Vriezeveen, the Netherlands), consisting of peat, sand and fertilizer, which had been steam-sterilized before use. Soon after emergence the seedlings were transferred to trays and later to pots when they had attained a suitable size. The experiments were performed in the greenhouse during the summer at a temperature of 20–23 °C without additional illumination.

The viruses used were:

- tobacco mosaic virus (TMV), a common strain, to test *N. tabacum* 'White Burley', *N. glutinosa* and *N. rustica;*
- cucumber mosaic virus (CMV), a yellow strain, maintained for many years by Dr

J. Dijkstra in this laboratory, to test *N. rustica;*
- red clover mottle virus (RCMV), Dutch isolate, supplied by Dr L. Bos, Institute of Phytopathological Research, Wageningen, to test *C. amaranticolor;*
- tomato spotted wilt virus (TSWV), Dutch isolate, supplied by Ir T. S. Ie of this laboratory, to test *N. rustica.*

Test plants were inoculated after having formed three to five leaves. Inoculations were made with sap expressed from infected plants, after prior dusting of the leaves with Carborundum 500 mesh.

All the batches of any one species were inoculted at the same time, thus allowing a comparison under identical environmental conditions. A number of uninoculated plants of each batch served as a control. The seedlings of each batch were examined for uniformity in morphology, colour of the leaves, etc., and their growth characteristics was compared with that of the plants of the other batches. After inoculation with a virus the various batches of each species or cultivar were compared to detect possible differences in their reaction to virus infection, such as number and appearance of local lesions or severity of systemic symptoms.

Numbers of local lesions on *N. glutinosa* resulting from infection with TMV were compared by estimating the 'local lesion index', i.e. the number of lesions formed on a leaf divided by the product of the length and width of the blade of that leaf. It was noticed that *N. glutinosa* plants from some sources were much easier to rub than plants from other sources. This observation prompted us to take this quality into account. Therefore plants of each source of this species were scored independently by two persons as 'easy', 'medium', or 'difficult' to be rubbed.

Results

C. amaranticolor. There were striking differences in growth habit among the sources. Some (Table 1: no. 3, 5, 12, 13) developed into very tall plants, with very little or no purple colour in the youngest leaves (Fig. 1, left). It is questionable whether those plants deserved the name *C. amaranticolor,* however, their taxonomic status was not investigated further.

Differences in leaf shape were noticed among the sources, especially concerning the base of the lamina. In some, the angle between base and petiole was 90 °C, but in others this angle was consistantly smaller (Fig. 2). This peculiarity did not coincide with the differences in growth habit and leaf colour noted above. In Table 1 the sources are grouped according to these characteristics.

Plants of all sources reacted with local lesions only following inoculation with RCMV, however, there were clear differences in their number and quality. Some (no. 1, 4, 12, 17, 18) consistently developed more lesions than others. A few (e.g. no. 4) reacted with large, easily countable lesions; others developed small lesions which were difficult to count (Table 1, Fig. 3). However, the size of the lesions was not correlated with the number of lesions formed per unit of leaf area. For quantitative work with RCMV we would have preferred no. 4 as assay host.

N. glutinosa. No differences in growth habit and form of the leaves were observed. However, some sources had smoother leaves than others and were thus easier to rub (Table 2).

Fig. 1. (Left). Growth habit of *C. amaranticolor* plants grown from seeds of two different origins. Left: origin no. 5, right: origin no. 1.

Fig. 2. (Right). Different shapes of leaves of *C. amaranticolor* plants grown from seeds of different origins.

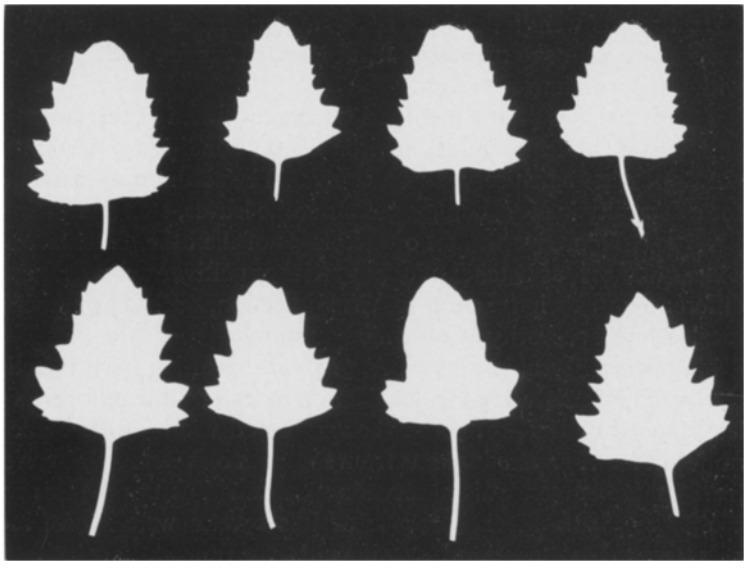

Fig. 1. (Links). Habitus van C. amaranticolor planten opgekweekt uit zaden van twee verschillende herkomsten. Links: herkomst no. 5, rechts: herkomst no. 1.

Fig. 2. (Rechts). Verschillende bladvormen van de diverse herkomsten van C. amaranticolor.

Fig. 3. Local lesions (formed by RCMV) on leaves of *C. amaranticolor* plants grown from seeds of origin no. 1, 4 and 12.

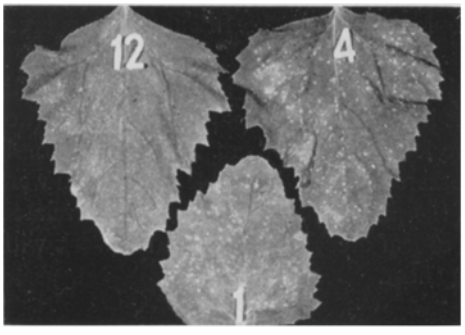

Fig. 3. Lokale lesies op bladeren van C. amaranticolor van drie herkomsten (no. 1, 4 en 12) na inoculatie met RCMV.

Fig. 4. Development of *N. rustica* plants grown from seeds of five origins. From left to right no. 5, 1, 2, 4 and 11 (see also Table 3).

Fig. 4. Ontwikkelingen van N. rustica-planten uit zaad van vijf verschillende herkomsten. Van links naar rechts no. 5, 1, 2, 4 en 11 (zie ook Tabel 3).

Table 1. The number and quality of local lesions due to RCMV on plants from seventeen sources of *Chenopodium amaranticolor*, and some features of their growth.

Source no.[1]	Growth habit[2]	Uniformity of germination[3]	Local lesions	
			number	quality
3	T	I	few	small and diffuse
5	T	F	moderate	somewhat diffuse
12	T	F	many	very small, difficult to count
13	T	R	moderate	very small, readily countable
1	N	F	many	large, somewhat diffuse
2[4]	N	F		
4	N	F	many	distinct, readily countable
6	N	I	few	distinct, readily countable
7[4]	N	F		
8	N	F	few	small, distinct
9[4]	N	F		
10	N	I	moderate	distinct – diffuse, countable
14	N	R	moderate	small
15	N	F	moderate	small, distinct
16	N	I	moderate	readily countable
17	N	F	many	distinct, readily countable
18	N	F	many	distinct – diffuse

[1] No. 11 did not germinate.
[2] T = tall plants, showing little purple colouration;
N = plants with normal growth habit and purple coloured top leaves.
[3] The seeds germinated regularly (= R), fairly regularly (= F) and irregularly (= I).
[4] Plants of this source were not tested with RCMV.

Tabel 1. Aantal en aard van de lokale lesies, die op zeventien Chenopodium amaranticolor herkomsten werden gevormd na inoculatie met rode klavermozaïekvirus (RCMV), en een paar waarnemingen over de groei van deze planten.

Leaves of all sources reacted to TMV with local lesions, but the numbers of lesions evoked using the same inoculum varied considerably in some cases (Table 2).

N. rustica. Plants from different sources exhibited a great diversity in their development. Some (no. 5 and 6) flowered quickly, some (no. 1 and 12) more slowly whereas the others remained longer in a rosette stage (Table 3, Fig. 4). Among the latter, some had flat leaves and others crinckled leaves. Differences in leaf width were noticed among the sources with flat leaves. Plants of sources no. 4 and 10 have broader leaves than those of no. 11 (Table 3).

Inoculated leaves of all sources invariably reacted to TMV with irregular necrotic spots surrounded by yellow discolourations, systemic symptoms consisting of mosaic and necrosis on the leaves and necrotic areas on the stems. The quickly developing plants showed yellowing around the necrotic spots on inoculated leaves earlier than those remaining rosetted for a longer period. The former showed necroses on the stems also earlier and more clearly.

After inoculation with CMV, the symptoms consisted of a systemic yellow mosaic only, however, there were differences in the severity of symptom expression: some

Tabel 2. The local lesion index[1] of sixteen sources of *N. glutinosa* and the smoothness of leaves to be rubbed.

Source no.[2]	Local lesion index[1]	Smoothness of leaves to be rubbed[3]
11	0–1	M
14	0–1	M
4	1–2	E
5	1–2	E
6	1–2	M
7	1–2	D
9	1–2	M
10	1–2	E
12	1–2	D
13	1–2	M
16	1–2	E
17	1–2	M
1	2–3	M
8	2–3	D
3	3–4	M
2	5–6	M

[1] The index is the number of local lesions divided by the product of the length and the largest width of the leaves.
[2] No. 15 did not germinate.
[3] E = easy; M = medium; D = difficult.

Tabel 2. De lokale lesie index van zestien herkomsten van N. glutinosa en de stroefheid van het bladoppervlak. De index is het aantal lokale lesies gedeeld door het produkt van bladlengte en grootste breedte van het blad.

Fig. 5. Symptoms produced on *N. rustica* plants by CMV. Top left: no. 5; top right: no. 1; middle: no. 2; bottom left: no. 4; bottom right: no. 11.

Fig. 5. Symptomen op planten van N. rustica na infectie met CMV. Boven links: no. 5; boven rechts: no. 1; midden: no. 2; beneden links: no. 4; beneden rechts: no. 11.

Fig. 6. Difference in size of leaves of *N. rustica* plants from two different origins. Top row: no. 4; bottom row: no. 5 (see also Table 3).

Fig. 6. Verschil in bladgrootte van N. rustica-planten van twee verschillende herkomsten. Bovenste rij: no. 4; onderste rij: no. 5 (zie ook Tabel 3).

Table 3. Eleven sources of *N. rustica* characterised by growth habit, leaf morphology and size, and sensitivity to infection with CMV and TSWV.

Source no.[1]	Growth habit and leaf morphology[2]	Yield of leaves per plant in grams[3]	Sensitivity[3] to	
			CMV	TSWV
5	Q, very quickly flowering	3.8	+	+
6	Q, very quickly flowering	4.0	+	+
1	Q, somewhat later flowering	10.5	+++	++
12	Q, somewhat later flowering	10.6	+++	++
9	I,	10.9	+++	++
8	I,	6.2	+++	++++
2	R, C	9.8	+	+++
3	R, C	8.8	+	+++
4	R, EB	16.0	+++	+++++
10	R, EB	15.9	++	++++
11	R, EN	16.8	++	+

[1] No. 7 did not germinate.
[2] Q = quickly developing plants.
R = plants remaining longer in the rosette stage.
I = plants intermediate between Q and R
EB = even, broad leaves.
EN = even, narrow leaves.
C = crinkled leaves.
[3] mean value of 3 plants.
[4] more '+' signs = more severe symptoms.

Tabel 3. De habitus, bladmorfologie, grootte, en gevoeligheid voor komkommermozaïekvirus (CMV) en tomatebronsvlekkenvirus (TSWV) van elf herkomsten van N. rustica.

sources (no. 1, 4, 8, 9, 12) showed a pronounced mosaic; other sources (no. 2, 3, 5, 6) reacted with a weak mosaic of mottling (Table 3, Fig. 5). No correlation was observed between symptom expression and growth habit.

Differences in the severity of symptoms were also observed following infection with TSWV, the symptoms consisting of systemic chlorosis and necrosis. As a rule, the sources characterized by early flowering became less necrotic than those with plants remaining rosetted longer (Table 3). Plants of the latter type sometimes showed top necrosis.

Generally the plants of the rosette type produced more leaf material than the early flowering plants (Table 3). This may make the former more useful for the propagation of viruses. Fig. 6. llustrates the differences in size of the leaves produced by two CMV infected plants of sources no. 4 and 5.

N. tabacum '*White Burley*'. Much variation was observed among the sources. Plants of most of the sources had sessile leaves embracing the stem to different extents (Fig. 7). Leaves of one source (no. 10) were petiolate, and as they were dark green it was supposed that the source was probably not 'White Burley' tobacco. Plants of some sources grew taller than those of others, and variations in leaf colour from light to dark green were observed.

Fig. 7. Differences in the shape of the basal part of leaves of *N. tabacum* 'White Burley' grown from seeds of four different origins. Top left (no. 3): clasping leaves with broad basal lobes; top right (no. 4): clasping leaves with small basal lobes; bottom left (no. 11): clasping leaves with very small basal lobes; right (no. 2); petiolated leaves.

Fig. 7. Verschillen in de vorm van het basale deel van de bladeren van N. tabacum 'White Burley' van 4 verschillende herkomsten. Boven links (no. 3): blad omvat de stengel half met brede lobben; boven rechts (no. 4): blad omvat de stengel half met smalle lobben; beneden links (no. 11): blad omvat de stengel met zeer smalle lobben; beneden rechts (no. 2): bladeren zijn gesteeld.

Fig. 8. Symptoms caused by TMV in *N. tabacum* 'White Burley' of two different origins. Left (no. 3): no leaf deformation; right (no. 4): leaf deformation.

Fig. 8. Symptomen op 'White Burley'-tabak afkomstig van twee verschillende herkomsten na intectie met TMV. Links (no. 3): geen bladdeformafie; rechts (no. 4); bladdeformatie.

Fig. 9. Top necrosis and death of a *N. tabacum* 'White Burley' plant (no. 12) kept at 28 °C after inoculation with TMV. Left: healthy plant; right: infected plant.

Fig. 9. Topnecrose en afsterven van een 'White Burley'-plant (no. 12), die na inoculatie met TMV bij 28 °C werd gehouden. Linls: gezonde plant; rechts: geïnfecteerde plant.

Plants of all sources except one reacted to TMV with systemic mosaic. However, some (no. 4, 7, 10, 11) showed leaf deformation as well, whereas others (no. 3) did not (Fig. 8). All plants of one source (no. 12) did not react in a way characteristic of 'White Burley'. At 28 °C these plants produced a few large necrotic spots on inoculated leaves, many small and very small local lesions were produced at 22 °C and 18 °C, respectively (Fig. 10). The plants kept at 28 °C, died suddenly from systemic infection about 12–14

Fig. 10. Local necrotic spots on a *N. tabacum* 'White Burley' plant (no. 12) after inoculation with TMV. From left to right: part of a healthy leaf, parts of leaves from plants kept at 18, 22 and 28 °C, respectively, after inoculation.

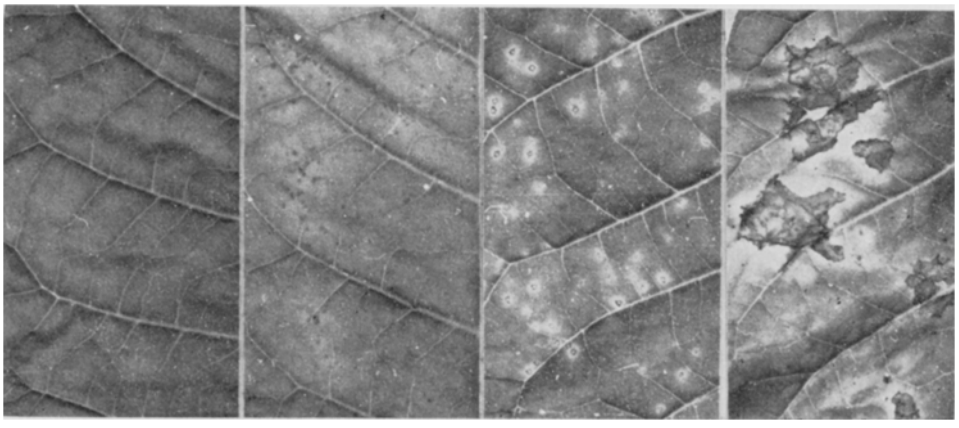

Fig. 10. Lokale necrotische vlekken op planten van 'White Burley'-tabak (no. 12) na inoculatie met TMV. Van links naar rechts: gedeelte van een blad van een niet-geïnoculeerde plant, gedeelten van bladeren van planten, die na inoculatie bij resp. 18, 22, en 28 °C stonden.

days after inoculation (Fig. 9). Assay on *N. glutinosa* leaves showed that TMV was present in the systemically infected leaves in high concentration when the plants were kept at 28 °C, and in low concentration when kept at 22 °C.

Discussion

The present results obtained with a few arbitrarily chosen test species clearly show that plants grown from the same named seeds from different sources, vary considerably in many respects. This conclusion supports earlier results obtained by Demski (1968) in his study of watermelon mosaic virus on *C. album* from different origins. There is no reason to believe that experiments with other species would not yield similar results.

In most publications concerning the symptomatology of viruses in artificial host ranges, although the external experimental conditions are often meticulously recorded, virtually no data are given about the origin of the plant species used. The results of this study clearly show that more information about the identity of test plants is essential and should be made available.

For comparing those viruses differing in their capacity to infect plants and to incite various kinds of symptoms, the use of genetically well-defined plant material is urgently needed. Only then can comparative symptomatology attain its full value in the characterization of viruses.

We do not believe that plant material used in virus studies should be characterized only on the basis of morphological and agricultural properties as is done by plant breeders when describing cultivars. Plant virologists may indicate that the cultivars or species used react after infection with one or more viruses in a characteristic way. While using for example the cultivar 'White Burley' for virus work, virologists must be aware that the batch used should react to a TMV infection in a prescribed manner. A reaction characteristic for an infection with a certain virus, must be a property for establishing and confirming the identity of the cultivar used in plant virus studies.

The results of Demski (1968) with *C. album*, and ours obtained with *C. amaranticolor* and *N. glutinosa* show that one source used as local lesion assay host may produce more and better recognisable lesions than another. Consequently it may be wise to do comparative testing to select the most appropriate host for a particular study. In such a selection, attention must also be paid to such characters as leaf size and ease of inoculation.

For the purpose of virus production a comparison of species or cultivars from different origins seems essential with respect to their capacity to produce quantities of leaf material. Although the amount of virus produced in leaf tissue was not investigated, differences in leaf size and number were observed in *N. rustica.*

It is reasonable to assume that the differences among sources described here may well depend on the environmental conditions, and the viruses or strains used. Hence it would be interesting to compare results obtained from experiments carried out in temperature and light controlled chambers, as well as of tests with the same sources of test plants carried out in different laboratories.

It would be desirable if different laboratories throughout the world would compare in a systematic way, sources of plant species used for virus work. These laboratories could serve as centres for the maintenance and distribution of seeds of a proven quality, and for information on specific questions regarding this type of work. However,

we doubt if there would be anyone willing to undertake such a laborious task. Therefore we hope that the results presented here will prompt other plant virologists to examine test plants in a similar manner and report the results, possibly propagating suitable species or cultivars for distribution among other virus workers.

Acknowledgments

The authors wish to express their gratitude to Drs R. Bercks, G. W. Cochran, R. I. B. Francki, A. H. Gold, B. D. Harrison, K. Helms, M. Hollings, B. Kassanis, H. Rønde Kristensen, K. Lindsten, J. P. MacKinnon, B. Nagaich, R. J. Shepherd, D. Spaar, K. Tomaru, V. Valenta and C. Wetter for providing seeds; to Drs L. Bos, J. Dijkstra and Ir T. S. Ie for providing virus isolates; to Mr G. Looijen and his staff for skilful raising of the plants; and to Drs L. Bos and A. Ziemiecki for their comments and help in preparing the manuscript.

Samenvatting

Een studie over de variaties van een aantal plantesoorten en hun bruikbaarheid in het virusonderzoek

Bij plantevirologisch onderzoek worden bepaalde plantesoorten en cultivars veelvuldig als toetsplant gebruikt. Het is echter niet bekend in hoeverre deze soorten en cultivars, in gebruik bij verschillende onderzoekers, genetisch identiek zijn. Derhalve is het ook niet bekend of zij op bepaalde virusinfecties gelijk reageren.

In het hier gepresenteerde onderzoek werden drie soorten en een cultivar van verschillende herkomst met elkaar vergeleken ten aanzien van hun reactie op een aantal virussen. Het onderzoek omvat *Chenopodium amaranticolor*, met lokale lesies reagerend op rode-klavervlekkenvirus (RCMV); *Nicotiana glutinosa*, met lokale lesies reagerend op tabaksmozaïekvirus (TMV); *N. rustica*, systemisch reagerend op TMV, komkommermozaïekvirus (CMV) en tomatebronsvlekkenvirus (TSWV); en *N. tabacum* 'White Burley', systemisch reagerend op TMV.

De resultaten van het onderzoek tonen aan dat er grote verschillen in reactie op één en dezelfde virusinfectie kunnen voorkomen tussen diverse herkomsten van eenzelfde soort of cultivar. Bovendien bleken sommige herkomsten op grond van verschillende overwegingen aantrekkelijker dan andere. Zo varieerde het aantal lokale lesies, gevormd op een blad van *C. amaranticolor* en *N. glutinosa*, al naar de herkomst van deze soorten zeer sterk (Fig. 3, Tabel 1 en 2). Nagenoeg alle herkomsten van *C. amaranticolor* reageerden met een eigen type van lokale lesies (Fig. 3, Tabel 1). Voorts bleken er verschillen te bestaan in de sterkte waarmee de symptomen tot uiting kwamen (Fig. 5 en 8), in de stroefheid der bladeren bij het inoculeren (Tabel 2), en in de hoeveelheid per plant geproduceerd bladmateriaal (Fig. 6, Tabel 3).

Andere geconstateerde verschillen betroffen habitus en ontwikkeling van de plant (Fig. 1, 4, 7 en 8, Tabel 3) en de vorm van de bladeren (Fig. 2 en 4). Een van de herkomsten van 'White Burley'-tabak reageerde op TMV met lokale lesies, gevolgd door topnecrose in plaats van met mozaïek en bladmisvorming, zoals de andere getoetste herkomsten van deze cultivars (Fig. 9, 10).

De resultaten van dit onderzoek wijzen uit dat voor de biologische karakterisering

van plantevirussen meer aandacht moet worden besteed aan de ervoor gebruikte toetsplanten. Enige voorstellen om te komen tot een betrouwbaarder toetsassortiment, worden in de discussie besproken.

References

Bos, L., 1967. Methods of studying plant as virus hosts. In: K. Maramorosch & H. Koprowski (Eds), Methods in virology I: 129–162.

Bos, L., Hagedorn, D. J. & Quantz, L., 1960. Suggested procedures for international identification of legume viruses. Tijdschr. PlZiekt. 66: 328–343.

Demski, J. W., 1968. Local lesion reactions of Chenopodium species of watermelon mosaic virus 2. Phytopathology 58: 1196–1197.

Frazier, N. W., 1974. Six new strawberry indicator clones evaluated for the detection and diagnosis of twelve grafttransmissible diseases. Pl. Dis. Reptr. 58: 28–31.

Fulton, J. P., 1960. Strawberry virus dissemination in Arkansas. Phytopathology 50: 477–480.

Harris, R. V. & King, M. E., 1942. Studies in strawberry diseases. V. The use of *Fragaria vesca* L. as an indicator of yellow-edge and crinckle. J. Pomol. 19: 227–242.

Kassanis, B. & Selman, J. W., 1947. Variations in the reaction of White Burley tobacco to the tomato aucuba mosaic virus and to some other strains of tobacco mosaic virus. J. Pomol 23: 167–170.

Köhler, E., 1953. Der Solanum demissum-Bastard 'A6' als Testplanze verschiedener Mosaikviren. Züchter 23: 173–176.

McRitchie, J. J. & Alexander, L. J., 1963. Host specific *Lycopersicon* strains of tobacco mosaic virus. Phytopathology 53: 394–398.

Mosch, W. H. M., Huttinga, H. & Rast, A. Th. B., 1974. Some chemical and physical properties of 18 tobacco mosaic virus isolates from tomato. Neth. J. Pl. Path. 74: 104–111.

Address

Laboratorium voor Virologie, Binnenhaven 11, Wageningen, the Netherlands.