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Reactions of Nicotiana species to potato viruses A, X and Y and tobacco mosaic virus in relation to their taxonomy and geographical origin

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Abstract

When testing the response of species of the genus *Nicotiana* to 14 isolates of potato viruses A (PVA), X (PVX) and Y (PVY) and tobacco mosaic virus (TMV), sections and section parts of the genus could be divided into five groups according to the overall reaction of their species. Species from arid regions of australia and belonging to the section *Suaveolentes* (subgenus *Petunioides*) were most sensitive and least resistant, whereas the sections *Paniculatae* (subgenus *Rustica*), *Tomentosae* (*Tabacum*) and *Noctiflorae* (*Petunioides*) appeared least sensitive and most resistant. Sixty-one percent of the accessions of the latter sections proved resistant to at least two of the viruses. The most resistant species have their main geographical distribution in the central Andes (southern Peru, Bolivia and north-western Argentina), where the viruses may have originated. One other resistant species was *N. africana* (*Suaveolentes*) indigenous to south-western Africa. The most sensitive American sections, viz. *Genuinae* (*Tabacum*) and *Trigonophyllae*, *Alatae*, *Acuminatae* and *Bigelovianae* (*Petunioides*), were generally more sensitive than species of the *Suaveolentes* section from outside the arid regions of Australia. The remaining part of the genus, viz. the American sections *Thyrsiflorae* and *Rusticae* (*Rustica*) and *Undulatae*, *Repandae* and *Nudicaules* (*Petunioides*) was intermediate between the latter group of *Suaveolentes* species and the resistant group of sections with regard to sensitivity and resistance, but had a high rate of tolerance to PVA, PVX and PVY and of hypersensitivity-associated resistance to TMV. The results indicate that the viral respons in the genus *Nicotiana* is mainly determined geographically and to a lesser extent taxonomically.

Additional keywords: centre of virus origin, hypersensitivity-associated resistance, immunity, resistance, resistance sources, sensitivity, test plants, tolerance.

Introduction

Several *Nicotiana* species are widely used as test plants in plant virology (Fulton, 1979), but the genus had not been explored at large for this purpose. Accessions from Australian deserts were recently found helpful for the detection and identification of some weakly aggressive viruses (i.e. viruses that have a narrow host range and with which infection of host plants often is difficult) that are otherwise difficult to isolate (Van Dijk et al., 1987). Other *Nicotiana* species might be of special interest for differentiation and separation of aggressive viruses that easily infect common *Nicotiana* species and that are thus readily detected. This led us to study the reactions of *Nico-*

tiana species to a number of aggressive viruses. Differential responses soon appeared to depend as much on the virus isolates as on the viruses or virus strains used. Preliminary results also showed a particular type of response to be more common in some sections of the genus than in others, whereas an even stronger correlation was found between response to virus and geographical origin of the species. This paper now reports on the variation within the genus *Nicotiana* in response to some aggressive viruses of potato and tobacco in relation to taxonomy and geographical distribution.

Materials and methods

Most accessions of the *Nicotiana* species tested were from the Tobacco Research Laboratory, Oxford, N.C., USA (Table 1, footnote 8). *N. tabacum* was from a seed stock commonly used at the Research Institute for Plant Protection, Wageningen. All 66 species recognized by Smith (1979), except *N. ameghinoi* (section *Noctiflorae*) and *N. longibracteata* (*Acuminatae*), and four additional species, viz. *N. palmeri* (*Trigonophyllae*), *N. sanderae* (*Alatae*), *N. angustifolia* (*Acuminatae*) and *N. eastii* (*Suaveolentes*) (see Van Dijk et al., 1987), were tested.

Table 1 lists the *Nicotiana* species taxonomically (Smith, 1979; V.A. Sisson, Tobacco Research Laboratory, personal communication) but for convenience in alphabetical order within sections.

Plants were grown in glasshouses at 18-22 °C (but incidentally up to 30 °C for potato virus X and tobacco mosaic virus), with additional illumination by 400 W SON-T high-pressure sodium lamps during winter to extend daylength to 16 h. When necessary for germination, seeds were soaked for one day in an aqueous solution of gibberellic acid (GA_3, 10^{-4}% w/v) before sowing. *Nicotiana* selections generally are genetically homogeneous, and the viruses used here are aggressive. Therefore per *Nicotiana* accession/virus-isolate combination usually one plant at the five-leaves stage was inoculated.

The strains and numbers of isolates of the potato viruses A, X and Y (PVA, PVX and PVY) and tobacco mosaic virus (TMV) (14 isolates in total) are mentioned in Table 1 (footnotes 2-7). Sources of inoculum were *N. tabacum* 'White Burley' for PVA, PVY and TMV, and *N. glutinosa* for PVX. About three weeks after inoculation systemic infection was judged by symptoms, by back-inoculation to *N. glutinosa* for TMV and to potato 'A6' for PVA, PVY^C and the PVY^N-isolate from potato 'Gineke', or by ELISA (Clark and Adams, 1977; for PVX and the other PVY-isolates). Symptoms on inoculated leaves were recorded for TMV only.

In this publication the following terms are used to describe the reactions of the *Nicotiana* species to the viruses. 'Sensitivity' refers to systemic infection accompanied by systemic symptoms, whereas 'tolerance' refers to systemic infection without systemic symptoms. The term 'low susceptibility' indicates a low systemic virus concentration. The term 'resistance' is used here to indicate lack of systemic infection. In case of absence of systemic infection by TMV, resistance is specified as 'hypersensitivity-associated resistance' when necrotic local lesions were present and as 'immunity' when local lesions were absent, although the inoculated leaves were not tested for the absence of virus (Table 1, footnote 1).

Results and discussion

Reactions of Nicotiana species. The results of extensive species reaction tests, using the above definitions, are summarized in Table 1.

Variations in reactions. Differences in reaction to inoculation were found to be common between accessions of the same species (Table 1) as found earlier with the same collection (Van Dijk et al., 1987). A striking example is *N. glutinosa* (subgenus *Tabacum*, section *Tomentosae*) with TMV (repeated experiments at 20 °C). All three accessions 24, 24A and 24B reacted with necrotic local lesions, but only accession 24 remained exempt from systemic infection thus showing hypersensitivity-associated resistance. Systemic lesions and resulting leaf malformation slowly developed in accession 24B, whereas lethal top necrosis developed in accession 24A within two weeks (Fig. 1). Lesion size (smallest in accession 24 and largest in 24A) also reflected differences in degree of susceptibility and/or sensitivity between the three accessions. Necrotic local lesions of *N. exigua* (subgenus *Petunioides*, section *Suaveolentes*)

Table 1. Response[1] of *Nicotiana* species and accessions to inoculation with viruses aggressive to the genus *Nicotiana*.

Subgenus Section Species-accession	Virus or virus strain					
	PVA[2]	PVY^C[3]	PVY^N[4]	PVY^O[5]	PVX[6]	TMV[7]
Subgenus *Rustica*						
Section *Paniculatae*						
N. benavidesii-8[8]	-,-,-	-,-,-	-,-,s	-,s,s	-	-i
N. cordifolia-15	s,s,-	-,s,-	S,-,s	s,s,s	s	S
N. cordifolia-15A	s,s,s	-,-,-	S,-,s	s,s,s	s	S
N. glauca-23	-,-,-	-,-,-	-,-,-	-,-,-	s	S
N. glauca-23A	-,-,-	-,-,-	-,-,-	-,-,-	-	-i
N. glauca-23B	-,-,-	-,-,-	-,-,-	-,-,-	-	s
N. glauca-23C	-,-,-	-,-,-	-,-,-	-,-,-	s	S
N. knightiana-27	-,-,-	-,-,-	-,-,s	-,-,-	S	-i
N. paniculata-40	s,s,s	-,-,-	S,-,s	-,s,s	S	s
N. paniculata-40A	s,s,-	s,-,-	S,-,s	-,s,s	s	-i
N. paniculata-40B	-,-,s	-,-,-	S,-,s	-,-,s	s	-i
N. paniculata-40C	s,s,s	-,s,s	S,-,S	s,S,s	S	-h
N. raimondii-45	-,-,-	-,-,-	-,-,-	-,-,-	S	S
N. solanifolia-52	.,.,.	.,.,.	.,.,.	.,.,.	s	s
Section *Thyrsiflorae*						
N. thyrsiflora-57	-,s,s	-,-,-	S,s,s	s,s,s	s	S
Section *Rusticae*						
N. rustica-44	-,s,s	-,s,-	S,S,s	-,s,s	S	S
N. rustica-48	s,s,s	-,-,-	S,s,s	s,s,s	S	S
N. rustica-49	-,s,s	-,s,-	s,s,s	-,s,s	S	S
N. rustica-49A	-,s,s	-,-,-	S,s,s	s,S,s	.	.
N. rustica-49B	-,s,s	s,s,s	S,S,S	-,S,S	S	S

For footnotes see page 348.

Table 1. (Continued)

Subgenus Section Species-accession	Virus or virus strain					
	PVA	PVY^C	PVY^N	PVY^O	PVX	TMV
Subgenus *Tabacum*						
Section *Tomentosae*						
N. glutinosa-24	-,-,-	-,S,-	S,-,S	S,S,-	S	-h
N. glutinosa-24A	-,-,-	-,-,-	S,-,S	S,S,S	S	S
N. glutinosa-24B	-,-,-	-,S,s	S,-,S	S,S,S	S	S
N. kawakamii-72	-,-,-	-,-,-	-,-,-	-,-,-	s	S
N. otophora-38	-,-,-	.,.,.	-,-,.	S,-,-	s	S
N. otophora-38A	-,-,-	-,-,-	-,-,.	-,-,-	S	S
N. otophora-38B	-,-,-	-,-,-	-,-,.	-,-,-	S	S
N. otophora-38C	-,-,-	-,-,-	-,-,.	-,-,-	S	S
N. setchellii-51	-,-,-	-,-,-	-,-,-	-,-,-	S	-i
N. tomentosa-58	-,-,-	-,-,-	-,-,-	-,-,-	.	.
N. tomentosa-58A	-,-,-	-,-,-	s,s,-	-,-,-	-	S
N. tomentosiformis-59	-,-,-	-,-,-	s,s,-	-,-,-	-	S
Section *Genuinae*						
N. tabacum cv. White Burley[9]	S,S,S	S,S,S	S,S,S	S,S,S	S	S
Subgenus *Petunioides*						
Section Undulatae						
N. arentsii-6	s,s,s	S,s,-	s,s,S	s,s,s	s	S
N. undulata-61A	s,S,s	s,s,-	s,S,s	s,s,s	S	S
N. undulata-61B	s,S,s	s,-,-	S,s,s	s,s,s	S	S
N. undulata-61C	s,s,s	s,s,s	S,-,s	S,s,s	S	.
N. wigandioides-63	-,-,-	-,-,-	s,-,s	-,s,s	.	.
Section *Trigonophyllae*						
N. palmeri-39	s,-,s	.,-,-	s,-,S	S,S,s	S	S
N. trigonophylla-60	-,s,s	-,-,-	S,S,S	S,s,S	S	S
Section *Alatae*						
N. alata-3	.,.,.	.,.,.	.,.,.	.,.,.	S	-h
N. alata-4	s,s,s	S,S,S	S,s,S	s,S,S	s	S
N. bonariensis-11	S,S,S	-,-,S	s,-,s	s,S,S	s	S
N. forgetiana-21A	s,s,s	-,-,-	S,-,s	S,S,S	S	-h
N. forgetiana-21B	s,s,s	-,s,-	s,-,s	S,s,s	.	.
N. langsdorffii-28A	S,S,s	-,-,-	S,-,S	S,S,S	S	S
N. langsdorffii-28B	S,S,S	-,S,-	S,-,S	S,S,S	S	S
N. longiflora-30	S,S,S	S,S,-	S,-,s	S,S,S	S	S
N. longiflora-30A	S,S,-	-,-,-	S,-,S	S,S,S	S	S
N. longiflora-30B	S,S,-	S,-,-	S,-,S	S,S,S	S	S
N. longiflora-30C	S,S,S	-,S,-	S,-,s	S,S,S	S	S
N. plumbaginifolia-43A	-,S,S	-,-,S	S,S,S	S,S,S	S	S
N. plumbaginifolia-43B	.,.,.	.,.,.	.,.,.	.,.,.	.	S
N. plumbaginifolia-43C	-,S,S	S,S,S	S,S,S	S,S,S	S	S
N. sanderae-50A	-,s,-	-,-,-	S,S,S	S,S,S	s	S
N. sanderae-50B	-,S,s	s,s,-	S,S,S	S,S,S	S	-h
N. sanderae-50C	-,S,s	s,s,-	S,S,S	S,S,s	S	S

For footnotes see page 348.

Table 1. (Continued)

Subgenus Section Species-accession	Virus or virus strain					
	PVA	PVY^{C}	PVY^{N}	PVY^{O}	PVX	TMV
Subgenus *Petunioides* (continued)						
Section *Alatae* (continued)						
N. sanderae-50D	-,s,s	s,s,-	S,s,S	S,S,s	S	S
N. sylvestris-56A	-,-,s	S,-,-	S,-,S	S,S,S	-	S
Section *Repandae*						
N. nesophila-34A	s,s,s	s,-,-	s,-,s	s,s,s	s	-h
N. repanda-46	-,S,s	-,S,-	S,S,S	S,S,S	S	-h
N. stocktonii-54	-,s,s	-,-,-	s,s,s	S,s,s	s	-h
Section *Noctiflorae*						
N. acaulis-1	-,-,-	-,-,-	-,-,-	-,-,-	.	.
N. noctiflora-35	.,.,.	.,.,.	.,.,.	.,.,.	.	-i
N. petunioides-42	-,-,-	s,-,-	s,-,s	-,s,s	s	s
Section *Acuminatae*						
N. acuminata-2	s,s,s	S,s,-	S,-,S	S,S,S	S	S
N. acuminata-2A	s,s,s	-,-,s	S,-,S	S,S,S	.	.
N. angustifolia-5	s,s,s	S,-,-	S,-,S	S,S,S	S	S
N. attenuata-7	s,s,s	-,-,-	S,-,S	S,s,S	.	.
N. corymbosa-16	-,s,-	-,-,-	S,-,s	s,s,s	S	S
N. linearis-29	s,s,-	s,.,-	S,-,s	s,s,S	S	S
N. miersii-33	s,-,-	-,.,-	s,-,S	s,s,s	S	S
N. pauciflora-41	s,-,s	-,S,-	S,-,S	S,S,S	S	S
N. spegazzinii-70	-,S,-	-,-,-	S,S,S	S,S,-	S	S
Section *Bigelovianae*						
N. bigelovii-10	s,s,s	S,s,-	s,-,s	s,s,s	S	S
N. bigelovii-12	s,s,s	-,S,S	S,-,S	s,s,s	S	S
N. bigelovii-13	s,s,s	-,-,S	S,S,S	s,s,s	S	S
N. clevelandii-14	s,s,s	-,S,S	.,-,S	S,S,S	S	.
Section *Nudicaules*						
N. nudicaulis-36	s,s,s	-,s,-	S,-,s	s,S,S	S	S
Section *Suaveolentes*						
N. africana-71	-,.,-	-,-,-	-,-,-	-,-,-	s	S
N. amplexicaulis-65	-,s,s	-,-,-	S,S,s	s,S,s	S	S
N. amplexicaulis-65A	S,S,s	-,-,-	S,S,S	S,S,S	S	S
N. benthamiana-9	S,s,S	-,-,S	S,-,S	S,S,S	S	S
N. benthamiana-9A	s,s,s	-,-,S	S,-,S	S,S,S	S	S
N. cavicola-68	-,s,S	-,S,-	S,S,S	S,S,S	S	S
N. debneyi-17	s,S,s	-,-,-	S,-,S	S,S,S	S	S
N. eastii-18	s,s,s	-,-,-	S,-,s	s,s,s	.	S
N. excelsior-19	s,s,s	-,-,-	S,-,S	S,S,S	S	S
N. excelsior-19A	s,s,s	-,-,-	S,-,S	S,S,S	S	S
N. exigua-20	S,-,s	-,-,S	S,-,S	S,S,S	s	S
N. exigua-20A	S,S,S	-,-,S	S,-,S	S,S,s	s	-h
N. fragrans-22	s,s,S	-,-,-	S,-,S	s,S,s	s	S
N. goodspeedii-25	s,s,s	s,-,s	S,-,S	S,S,S	s	-h

Table 1. (Continued)

Subgenus Section Species-accession	Virus or virus strain					
	PVA	PVY^C	PVY^N	PVY^O	PVX	TMV
Subgenus *Petunioides* (continued)						
Section *Suaveolentes* (continued)						
N. gossei-26	s,s,s	-,-,-	S,-,S	S,S,S	S	-h
N. hesperis-67	s,s,s	-,S,-	S,S,S	S,s,s	s	S
N. hesperis-67A	S,S,S	-,-,-	S,S,S	S,S,S	S	S
N. ingulba-64	-,s,S	S,s,-	S,S,S	S,S,S	S	S
N. maritima-31	s,s,-	-,-,s	S,-,S	S,s,S	s	S
N. megalosiphon-32	S,S,S	-,S,-	S,-,S	S,S,S	S	S
N. megalosiphon-32A	s,s,s	-,S,-	S,S,S	S,S,S	.	.
N. occidentalis-37	S,s,s	-,S,-	S,-,S	S,S,S	S	S
N. occidentalis-37A	S,S,S	-,S,-	S,-,S	S,S,S	s	S
N. occidentalis-37B	s,S,s	S,S,-	S,-,S	S,S,S	S	S
N. rosulata-53	-,s,s	-,.,-	S,S,S	S,S,S	S	S
N. rosulata-53A	s,s,s	-,S,S	S,S,s	S,S,S	S	S
N. rotundifolia-47	-,s,s	S,-,-	S,S,S	S,S,S	S	S
N. rotundifolia-47A	-,s,s	S,-,-	S,S,S	S,S,S	S	S
N. simulans-66	S,S,S	-,S,-	S,S,S	S,S,S	S	S
N. suaveolens-55	-,s,s	-,-,-	S,S,S	s,s,S	s	S
N. suaveolens-55A	-,s,s	-,-,-	S,S,S	s,s,S	S	S
N. suaveolens-55B	-,S,s	-,s,-	S,s,S	S,s,S	S	S
N. suaveolens-55C	-,s,s	-,-,s	S,s,S	S,s,S	S	S
N. umbratica-69	-,-,.	-,-,-	S,s,.	s,s,-	S	S
N. velutina-62	s,s,s	-,S,-	S,S,s	S,s,s	S	S
N. velutina-62A	-,S,S	-,S,-	S,S,S	S,s,s	S	S
N. velutina-62B	-,s,s	-,.,-	S,S,S	S,s,s	S	S

[1] Symbols: S = sensitivity (systemic symptoms); s = tolerance (symptomless systemic infection); - = resistance (no systemic infection); -h = hypersensitivity-associated resistance (necrotic local lesions and no systemic infection, indicated for TMV only); -i = immunity (no local lesions and no systemic infection, indicated for TMV only; lack of latent local infection not checked); . = not tested.

[2] Isolates of potato virus A (Bartels, 1971) from potato cvs Advira, Lichte Industrie and Saucisse Rouge, respectively.

[3] Isolates of potato virus Y^C (De Bokx and Huttinga, 1981) from potato cvs Lichte Rode Star, Vroege Paarse and Zeeuwse Blauwe, respectively.

[4] Isolates of potato virus Y^N (De Bokx and Huttinga, 1981) CH605 (Gugerli strain) and from potato cvs Gineke and Record, respectively.

[5] Isolates of potato virus Y^O (De Bokx and Huttinga, 1981) from potato cvs Bintje, Libertas and Paul Kruger, respectively.

[6] One isolate of the 'Cockerham group 1 strain' (Cockerham, 1955) of potato virus X (Bercks, 1970).

[7] One isolate (U_1) of the 'common strain' of tobacco mosaic virus (Zaitlin and Israel, 1975), kindly provided by Dr J. Dijkstra, Wageningen Agricultural University.

[8] Code numbers from Tobacco Research Laboratory; additions A, B, etc. denote different accessions.

[9] Seed stock of Research Institute for Plant Protection.

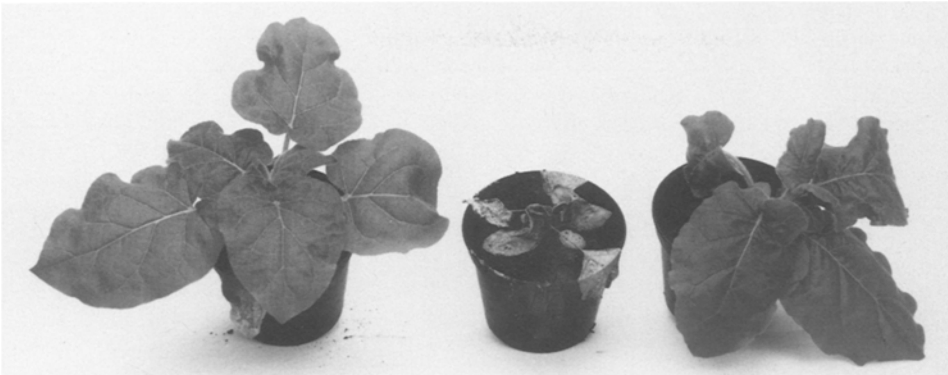

Fig. 1. Plants of *N. glutinosa* accessions with different reactions after inoculation with tobacco mosaic virus. All three accessions reacted with necrotic local lesions but only accession 24 (left) remained free from systemic infection (hypersensitivity-associated resistance). Accession 24B (right) slowly developed necrotic lesions and malformation in non-inoculated leaves while accession 24A (middle) rapidly died from systemic necrosis.

developed in accession 20A after inoculation with TMV and systemic infection did not occur (hypersensitivity-associated resistance), whereas accession 20 reacted with non-necrotic local and systemic symptoms to the virus (Table 1).

Great differences were also observed in the responses to different isolates of the same virus. For example, *N. paniculata*-40A (subgenus *Rustica*, section *Paniculatae*) became systemically infected by 2, 1, 2 and 2 out of 3 isolates each of PVA, PVY^C, PVY^N and PVY^O, respectively, and showed symptoms to one isolate of PNY^N only (Table 1).

Comparison between the overall responses of the sections. The differences observed between accessions and between virus isolates imply that general conclusions concerning virus/genus interaction can only be drawn after studying large numbers of accession/virus-isolate combinations. Per taxonomic section the percentages of sensitivity, tolerance and resistance of the accessions to the 14 virus isolates were therefore calculated (assigning equal weight to virus isolates), and the number of virus isolates inducing these reaction types recorded (Table 2). This provides an indication of the overall vulnerability (susceptibility plus sensitivity) of the species of the sections to the viruses used. High percentages of sensitivity together with low percentages of resistance, accompanied by high and low numbers, respectively, of isolates concerned, was characteristic for sections *Genuinae* (*Tabacum*) (only one accession tested) and *Trigonophyllae*, *Alatae*, *Acuminatae*, *Bigelovianae* and *Suaveolentes* (*Petunioides*). These sections could be designated as 'sensitive sections'. The reverse held for sections *Paniculatae* (*Rustica*), *Tomentosae* (*Tabacum*) and *Noctiflorae* (*Petunioides*), now called 'resistant sections'. The remaining sections had intermediate percentages of sensitivity and resistance but high percentages of tolerance and are now mentioned 'tolerant sections'.

Since the results obtained with the four viruses were averaged, the question arises whether this tendency holds for each of the viruses. Therefore the average response

Table 2. Cumulated systemic response in sections of the genus *Nicotiana* to inoculation with potato viruses A, X and Y and tobacco mosaic virus[1].

Subgenus Section	Number of accessions tested	Sensitivity		Tolerance		Resistance	
		S (%)	number of virus isolates	s (%)	number of virus isolates	– (%)	number of virus isolates
Subgenus *Rustica*							
Section *Paniculatae*	14	9	5	27	12	64	14
Section *Thyrsiflorae*	1	14	2	57	8	29	4
Section *Rusticae*	5	26	7	49	12	25	5
Subgenus *Tabacum*							
Section *Tomentosae*	12	21	8	4	4	75	14
Section *Genuinae*	1	100	14	0	0	0	0
Subgenus *Petunioides*							
Section *Undulatae*	5	21	8	60	13	19	8
Section *Trigonophyllae*	2	44	8	26	6	30	6
Section *Alatae*	19	60	14	17	12	23	9
Section *Repandae*	3	24	9	45	11	31	6
Section *Noctiflorae*	3	0	0	26	7	74	13
Section *Acuminatae*	9	43	12	27	10	30	8
Section *Bigelovianae*	4	41	11	44	9	15	4
Section *Nudicaules*	1	36	5	43	6	21	3
Section *Suaveolentes*	37	54	14	21	12	25	13

[1] Data are summarized from Table 1. Average percentages of accession/virus-isolate combinations were calculated by assigning equal weight to virus isolates.

per virus was calculated. As done earlier (Van Dijk et al., 1987), the large and only non-American *Suaveolentes* section (Goodspeed, 1954) was also judged separately from the American sensitive sections, and divided into one part comprising the species from arid regions of Australia and another one with species from elsewhere. When the two parts of the *Suaveolentes* section and the three groups, into which the other sections of the genus had been divided, were listed in order of decreasing sensitivity, the same sequence was obtained for each of the viruses with some minor deviations only (Table 3, reaction groups A-E). The species from arid regions of Australia (group A) constitute the most sensitive part of the genus while the *Suaveolentes* species from elsewhere (C) on an average are less sensitive than those of sensitive American sections (B). The same conclusion was drawn previously when the genus was challenged with a group of weakly aggressive viruses. The differences in response to those viruses (Van Dijk et al., 1987) were larger than to the aggressive viruses now used. The latter viruses, in turn, appear more suitable for the detection of resistance than of sensitivity. Of the three sections in the resistant group E, viz. *Paniculatae*, *Tomentosae* and *Noctiflorae*, 61% of the accessions proved resistant to each isolate of at least two of the four viruses applied (Table 3). *N. africana*-71 (*Suaveolentes*), indigenous to south-western Africa

Table 3. Division of the genus *Nicotiana* into five reaction groups according to its response to inoculation with potato virus A (PVA), potato virus Y (PVY), potato virus X (PVX) and tobacco mosaic virus (TMV).

Reaction group[1]	Number of accessions tested	PVA			PVY			PVX			TMV				Average[3]			Accessions resistant to at least two viruses (%)
		S(%)[2]	s(%)	–(%)	S(%)	s(%)	–(%)	S(%)	s(%)	–(%)	S(%)	s(%)	-h(%)	-i(%)	S(%)	s(%)	–(%)	
A: *Suaveolentes* spp. from arid regions of Australia[4]	21	27	58	15	64	8	28	90	10	0	95	0	5	0	69	19	11	0
B: Sensitive American sections[5]	35	28	51	21	55	17	28	87	10	3	90	0	10	0	65	19	16	0
C: *Suaveolentes* spp. from elsewhere[6]	16	26	55	19	47	17	37	50	50	0	87	0	13	0	52	30	17	6
D: Tolerant American sections[7]	15	7	71	22	21	52	27	69	31	0	75	0	25	0	43	38	19	0
E: Resistant American sections[8]	29	0	17	83	11	15	74	42	38	19	52	15	7	26	26	21	52	61

[1] Groups of sections and section parts differing in their overall virus reaction (see Table 1 and 2), listed in order of decreasing sensitivity. Data are summarized from Table 1.
[2] Figures represent percentages accession/virus-isolate combinations with reactions as follows: S = sensitivity; s = tolerance; – = resistance; -h = hypersensitivity-associated resistance; -i = immunity (see also Table 1, footnote 1).
[3] Average values calculated by assigning equal weight to viruses.
[4] The following species that are restricted to central and western Australia (Burbidge, 1960): *N. benthamiana*, *N. cavicola*, *N. excelsior*, *N. gossei*, *N. hesperis*, *N. ingulba*, *N. occidentalis*, *N. rosulata*, *N. rotundifolia*, *N. simulans*, *N. umbratica* and *N. velutina*.
[5] *Genuinae* (subgenus *Tabacum*) and *Trigonophyllae*, *Alatae*, *Acuminatae* and *Bigelovianae* (*Petunioides*).
[6] *N. africana*, *N. amplexicaulis*, *N. debneyi*, *N. eastii*, *N. exigua*, *N. fragrans*, *N. goodspeedii*, *N. maritima*, *N. megalosiphon* and *N. suaveolens*.
[7] *Thyrsiflorae* and *Rusticae* (*Rustica*) and *Undulatae*, *Repandae* and *Nudicaules* (*Petunioides*).
[8] *Paniculatae* (*Rustica*), *Tomentosae* (*Tabacum*) and *Noctiflorae* (*Petunioides*).

(Merxmüller and Buttler, 1975), was the only other species resistant to at least two of the viruses (Table 1 and 3).

Our results are also in line with the literature on resistance to tobacco viruses. Eleven out of fourteen *Nicotiana* accessions that were found resistant to PVY (probably from tobacco, Sievert, 1972) and eight out of ten *Nicotiana* species that proved resistant to tobacco etch virus (see Stavely, 1979) are from our resistant group E. The *Nicotiana* species reported as most susceptible to TMV by Holmes (1951) preponderantly belong to our sensitive groups A, B and C (sensitive American sections and the *Suaveolentes* section, Table 3).

Geographical distribution of reaction types. The American sections *Paniculatae*, *Tomentosae* and *Noctiflorae* that constitute our group E, characterized by high numbers of species with resistance, each belong to a different subgenus (Table 3). This means a poor correlation between resistance and taxonomy of *Nicotiana* species. However, a strong correlation seems to exist between resistance and geographical origin of the species. The most resistant species of group E (Table 1) appear to be mainly confined to the central Andes, viz. southern Peru, Bolivia and north-western Argentina (Goodspeed, 1954; Ohaski, 1976). Unfortunately, precise geographical data on the accessions of the Tobacco Research Laboratory are not available, and we therefore cannot verify whether indeed (see next section and Figs. 2 and 3) at first tolerance or hypersensitivity-associated resistance and thereafter sensitivity of accessions become prominent with increasing distance from the apparent centre of resistance. But the fact that the main geographical range of the most sensitive species of group B (Table 1 and 3) is in Central and North America and eastern South America (Goodspeed, 1954) is in accordance with this assumption. The correlation between sensitivity and geography is most clearly demonstrated by the species from Australian deserts, both in this study (Table 3, group A) and in earlier work (Van Dijk et al., 1987).

The distribution of TMV-resistant *Nicotiana* species was investigated earlier by Holmes (1951). The occurrence of distinct types of resistance and hypersensitivity especially in Peru and adjacent countries led him to suggest that this area is the centre of origin of the virus. The prevalence of resistant *Nicotiana* species in the central Andes, as further demonstrated in our study, suggests this area to be the centre of origin of PVA, PVX and PVY, as well as of TMV. Solanaceous accessions from this area seem to be promising sources for resistance breeding. All present plant viruses might even have originated in the central Andes, but this should be tested further with viruses of non-solanaceous taxa.

Adaptation to infection pressure. On the above assumption, prevalent virus resistance in the Central Andes might have resulted from high infection pressure during host evolution. The viral response of the groups A-E (Table 3) may then be plotted as a function of this exposure to virus infection, which we assume to have reached different levels during co-evolution of virus and hosts, depending on duration and degree of infection pressure in the geographical areas concerned. This is done for the closely related PVA and PVY with increasing loss of sensitivity (Fig. 2, A-E), first associated with a stage of increasing tolerance (Fig. 2, A-D), followed by another stage where the tolerance is lost in favour of resistance (Fig. 2, D-E). Results with PVX are comparable to those with PVA and PVY (Table 3). With PVY, where low susceptibility could be

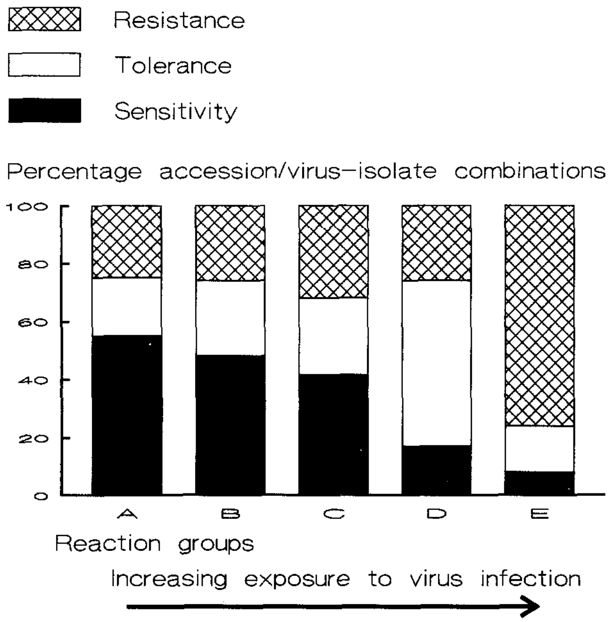

Fig. 2. Postulated adaptation of the genus *Nicotiana* to increasing exposure to infection by potato viruses A and Y during its evolution. The figure is based on viral response of the groups of sections and section parts A-E distinguished in Table 3. Duration and degree of infection pressure is assumed to increase from A to E as evidenced by decreasing sensitivity. In a first stage (A-D) tolerance increases and in a second stage (D-E) the tolerance is replaced by resistance. Deviations in group C are largely due to the resistant species *N. africana* that fits best in group E (see text).

measured semi-quantitatively by ELISA absorbance values, 39% of the tolerant accessions of group E showed low susceptibility, while ten percent or usually much less of the tolerant accessions of the other groups or the sensitive accessions of any group did so (Table 4). Thus, absence of symptoms in some cases, but mainly in the resistant group E, is due to low susceptibility rather than tolerance. Likewise, accessions latently infected by TMV, found exclusively in group E (Table 3) and corresponding with the highest infection pressure (Fig. 3, E), usually contained little virus. Although tested for one isolate of TMV only, species may not have developed true tolerance to the virus. Hypersensitivity-associated resistance to TMV, however, like tolerance to the other viruses, most frequently occurs at moderate infection pressure (Figs. 2 and 3, C-D). Both defense mechanisms seem to be effective at low or moderate levels of infection pressure. They still imply susceptibility and may indicate an equilibrium between virus and host. Since any infection will have harmful effects, immunity is likely to be favoured when infection pressure increases further.

Implications for experimental virology. The group E, comprising resistant species (Table 3), seems to be the most useful part of the genus for the differentiation of aggressive viruses. However, wide variation in response to different isolates of the same virus or virus strain (Table 1) implies that particular accessions found to differentially

Table 4. Distribution of sensitivity (S)[1], tolerance (s), low susceptibility (l)[2] and resistance (–) in reaction groups A-E[3] of the genus *Nicotiana* to potato virus Y[4].

Reaction group	Sensitivity				Tolerance				Resistance	
	S	S (%)	l	l (%)	s	s (%)	l	l (%)	–	– (%)
A	82	86	1	1	12	13	0	0	1	1
B	116	74	3	3	39	25	1	3	1	1
C	57	72	0	0	17	22	1	6	5	6
D	22	29	1	5	49	65	5	10	4	5
E	20	16	2	10	28	22	11	39	80	63

[1] For description of the terms sensitivity, tolerance and resistance see Table 1, footnote 1; numbers and percentages of accession/virus-isolate combinations were calculated from Table 1.

[2] Accessions of species, either sensitive or tolerant to the virus isolate applied, were regarded lowly susceptible when the ELISA absorbance value after one hour substrate incubation was between 0.25 and 2.00 (not shown in Table 1).

[3] See Table 3.

[4] Isolates CH605 and from potato cvs Record (PVY^N) and Bintje, Libertas and Paul Kruger (PVY^O).

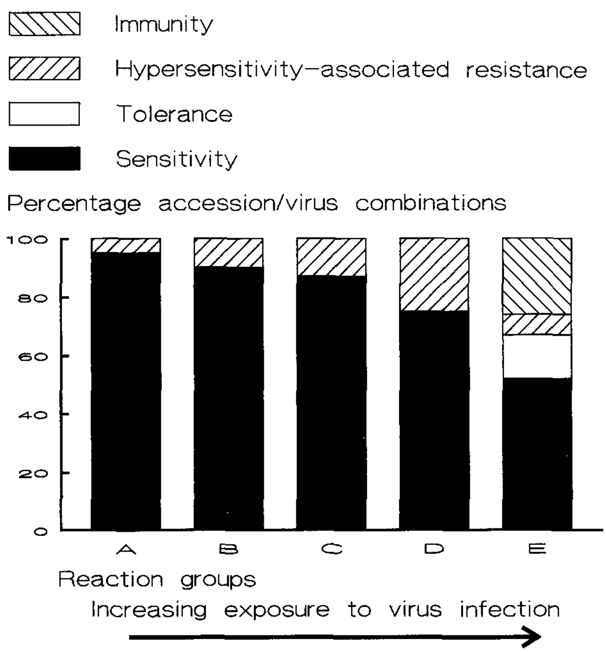

Fig. 3. Postulated adaptation of the genus *Nicotiana* to increasing exposure to infection by tobacco mosaic virus during its evolution. Increase of infection pressure, as deduced from loss of sensitivity, is from reaction group A to E (see also Fig. 2). Note a first stage (A-D) during which hypersensitivity-associated resistance increases, and a second stage (D-E) where this type of resistance is largely replaced by tolerance and immunity. Symptomless infections in group E may be due to low susceptibility instead of to true tolerance (see text).

react with the few isolates tested per virus cannot always be reliably used to differentially identify such viruses.

In our tests, several accessions were not systemically invaded by PVX, TMV, or both (Table 1). With such accessions elimination of highly infectious viruses from a virus or vector culture might be achieved. The suitability of *Nicotiana* accessions from Australian deserts as indicator hosts for virus detection and identification by symptoms (Van Dijk et al., 1987) is augmented by their sensitivity to the viruses used in this study (Table 3, group A).

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Samenvatting

Reacties van Nicotiana-soorten op aardappelvirussen A, X en Y en tabaksmozaïekvirus in samenhang met hun taxonomie en geografische herkomst

Na inoculatie van een grote collectie *Nicotiana*-soorten met 14 isolaten van de aardappelvirussen A (PVA), X (PVX) en Y (PVY) en tabaksmozaïekvirus (TMV), konden de secties of sectiedelen van het genus op basis van de gemiddelde reactie van hun soorten in vijf groepen worden verdeeld. Soorten uit Australische woestijngebieden en taxonomisch behorend tot de sectie *Suaveolentes* (subgenus *Petunioides*) bleken het meest gevoelig en het minst resistent, terwijl de secties *Paniculatae* (subgenus *Rustica*), *Tomentosae* (*Tabacum*) en *Noctiflorae* (*Petunioides*) het minst gevoelig en het meest resistent waren. Van de collectienummers van de laatstgenoemde secties bleek 61% resistentie tegen minstens twee van de virussen te bezitten. De meest resistente soorten hebben hun verspreidingsgebied vooral in het centrale deel van het Andesgebergte (het zuidelijk deel van Peru, Bolivia en noord-westelijk Argentinië). Mogelijk is dit het ontstaansgebied van deze virussen. De enige andere resistente soort was *N. africana* (*Suaveolentes*) uit zuid-westelijk Afrika. De meest gevoelige Amerikaanse secties, te weten *Genuinae* (*Tabacum*) en *Trigonophyllae*, *Alatae*, *Acuminatae* en *Bigelovianae* (*Petunioides*), waren gemiddeld gevoeliger dan *Suaveolentes*-soorten die niet uit de Australische woestijnen afkomstig zijn. Het resterende deel van het genus, bestaande uit de Amerikaanse secties *Thyrsiflorae* en *Rusticae* (*Rustica*) en *Undulatae*, *Repandae* en *Nudicaules* (*Petunioides*), stond met betrekking tot gevoeligheid en resistentie tussen laatstgenoemd deel van de sectie *Suaveolentes* en de groep resistente secties in, maar vertoonde in hoge mate tolerantie voor PVA, PVX en PVY en met overgevoeligheid samengaande resistentie voor TMV. Uit de resultaten blijkt dat de reacties van het genus *Nicotiana* op virussen vooral geografisch bepaald zijn en in mindere mate taxonomisch.

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