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Computer Aided Evaluation of Differences in Host Reactions between Isolates of Turnip Mosaic Virus from *Sisymbrium loeselii*

J. BRČÁK and J. BRČÁK JR.

Institute of Experimental Botany, Czechoslovak Academy of Sciences, Praha*

Abstract. Twenty three isolates of turnip mosaic virus (TuMV) obtained from spontaneously infected plants of *Sisymbrium loeselii* JUSL. were serologically related, but differed in reactions of eleven host plants. Susceptibility and sensitivity of each host for each TuMV isolate were classified by one of six degrees (0 to 5) respectively. Similarities of isolates (as compared in 253 pairs) were evaluated by means of a computer; for this purpose the source program MINDIF has been elaborated using the universal program language Algol 60. A table of differences between isolates was obtained and distribution of isolate pairs dependent upon the difference values was stated. The fitness of hosts for differentiating TuMV isolates was ascertained quantitatively. No relation of isolate similarity to geographical indices could be established.

A considerable variability of turnip mosaic virus (TuMV) strains may lead away the determination of TuMV, if differential hosts only have been used. Some experienced TuMV hosts may prove by their reactions to be unreliable. *E.g.* TOMPKINS (1939) and USCHDRAWEIT and VALENTIN (1957) reported *Nicotiana glutinosa* L. as fully unsusceptible for some TuMV isolates; the same has been stated of several Bohemian TuMV isolates from *Sisymbrium loeselii* JUSL. by PROCHÁZKOVÁ (1980). *Nicotiana tabacum* L. represents an important differential host of TuMV by its necrotic local lesion reaction. However, even this plant species does not show a fully uniform reaction to all TuMV strains. TOMPKINS (1939) observed on tobacco local lesions of different size with two TuMV strains, LAPIERRE and GRISON (1969) obtained no symptoms at all in tobacco 'Samsun' inoculated with an isolate from *Alliaria officinalis* ANDR. apparently belonging to the TuMV group. Also TuMV isolates dealt with in the present paper evoke lesions in tobacco 'Samsun' of a different character (Fig. 1). Thus, one cannot rely on differential hosts with particular TuMV strains sometimes showing reactions similar to several other members of the Potyvirus group. Some strains of the bean yellow mosaic virus (BYMV) are able to cause local rings or chlorotic local lesions in *N. tabacum*, but no infection in *N. glutinosa*, and may not be transmissible to some cultivars of pea (THOMAS and ZAUMEYER 1953,

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* *Address:* Na Karlovce 1a, 160 00 Praha 6, Czechoslovakia.

ZAUMEYER and FISHER 1953). On the contrary some TuMV strains can infect pea plants (first reported by FISCHER and LOCKHART 1976). Reactions of *Phaseolus vulgaris* L. cultivars may also be confusing, because there are strains of BYMV to which some bean cultivars are susceptible to local lesion infection only (ZAUMEYER and FISHER 1953). Only four of our TuMV isolates could not be transmitted to *P. vulgaris* cv. Prince and all the remaining ones caused local chlorotic lesions or rings on this plant. However, TWARDOWICZ-JAKUSZ and ZIELIŃSKA (1979) described a TuMV strain from carrot being sometimes able to cause necrotic local lesions and prospective systemic necrosis in stems and leaves of *P. vulgaris* cv. Złota Saxa. Reactions of *Trifolium incarnatum* L. to some strains of TuMV and BYMV may be similar. The differentiation of BYMV from TuMV by susceptibility of *Vicia faba* L. to BYMV and not to TuMV (PROVVIDENTI 1978) cannot be fully accepted, because some TuMV strains also can infect *V. faba*; hitherto local infection only has been proved by PROCHÁZKOVÁ (1980).

Another member of the Potyvirus group, the lettuce mosaic virus, might be distinguished by its systemic infection in *Chenopodium quinoa* WILLD. and lesions in *Phaseolus vulgaris* (PROVVIDENTI 1978); however, there are strains of TuMV reacting identically.

Two main aims are dealt with in the present paper: (a) to verify serologically that all single-lesion isolates from *S. loeselii* belong to TuMV and (b) to evaluate the variability of TuMV by computer aided comparison of isolates based on different degrees of susceptibility and sensitivity of selected hosts; this also enabled the classification of hosts as being more or less suitable for differentiation of TuMV strains.

MATERIAL AND METHODS

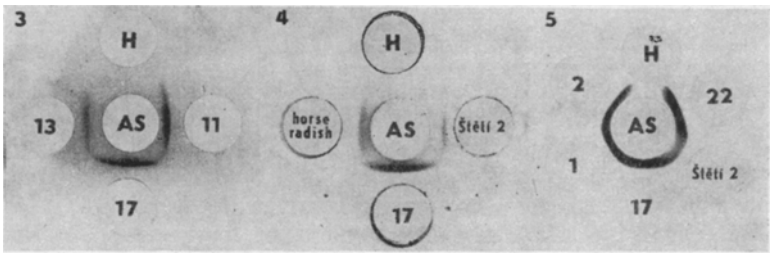
Twenty three single-lesion isolates obtained from spontaneously infected *S. loeselii* in Bohemia at localities reported by POLÁK and CHLUMSKÁ (1978) and investigated for our purposes by PROCHÁZKOVÁ (1980) are dealt with. Table 2 contains consecutively numbered localities and hosts as well as the given values of susceptibility and sensitivity identical to that in the last mentioned paper, in which the values (degrees) have been explained. However, only some isolates and hosts were selected for our investigation.

The isolate 17 (Pardubice 1) propagated in *N. glutinosa* plants was used for virus purification, performed according to CHOI *et al.* (1977). The purified virus was checked up with an electron microscope; diluted suspensions were negatively stained with potassium phosphotungstate, pH 6.8 (Fig. 2). Immunization of rabbits and prepared antisera were conformed to the procedures by CHOI *et al.* (1978). Ouchterlony double diffusion tests were performed according to PAPA *et al.* (1973), but antigens from *Petunia hybrida* hort. ex VILM. were prepared from pyrrolidine-treated leaf extracts as diffusible antigenic fragments (SHEPARD 1970). Serological reactions were controlled by normal serum, extracts from healthy plants, other isolates of TuMV, and TuMV unrelated antigens. Precipitation bands were stained with naphthalene black 12B.

All isolates were also examined by means of electron microscopy of diluted suspensions from infected petunia leaves. The relative virus concentrations in systemically infected petunia plants were compared with four isolates by

numbers of local necrotic lesions on Samsun tobacco leaves rubbed with diluted crude sap (1 g of fresh leaves was homogenized with 100 ml of water).

Reactions of each host to each virus isolate are expressed by one of six degrees of susceptibility and by one of six degrees of sensitivity (Table 2). The similarity of isolates was determined quantitatively for all possible pairs of virus isolates with regard to their reactions on all hosts used. Let's



Figs. 3, 4, 5. Results of serological double diffusion tests with pyrrolidine treated antigens. Antiserum in the central well, numbers of depots correspond to isolate numbers. H-healthy plants.

presume that m of virus isolates $I_1, I_2, \ldots, I_m$ were investigated on n of hosts $H_1, H_2, \ldots, H_n$. Let's have two virus isolates $I_k, I_l (k, l \in \{1, 2, \ldots, m\}, k \neq l)$ that were tested on all n hosts. Let the host reaction $H_i (i \in \{1, 2, \ldots, n\})$ to the virus isolate I_k or I_l be evaluated by means of the degrees of susceptibility V_{ki} and V_{li} respectively and sensitivity C_{ki} and C_{li} respectively. Let's use the symbol P_{kl} for the similarity of isolates I_k and I_l and let's define:

$$P_{kl} \underset{Df}{=} \sum_{i=1}^{n} (|V_{ki} - V_{li}| + |C_{ki} - C_{li}|) .$$

Evaluating the similarity of isolates in pairs we get out of the values P_{kl}: A minor value indicates a greater similarity of host reactions to isolates I_k and I_l.

To ascertain quantitatively how a given host is able to distinguish between virus isolates let's designate the ability to differentiate a given group of virus isolates by R_i and let's define:

$$R_i \underset{Df}{=} \sum_{j=1}^{m-1} \sum_{k=j+1}^{m} (|V_{ji} - V_{ki}| + |C_{ji} - C_{ki}|) .$$

A greater R_i value means a greater ability of the host H_i to differentiate the given isolates.

With many virus isolates and many hosts a manual calculation would be cumbersome to evaluate the similarity of isolates, to sort pairs of isolates according to their similarity and to ascertain the fitness of hosts used. Thus, computer aid is applicable for these purposes. A computer Tesla 200 was employed for our investigation.

The program MINDIF (Minimum Differences) has been worked out using the universal program language Algol 60 which enables the dynamic dec-

laration of arrays (Table 1). This is advantageous for the universal program MINDIF, because various numbers of virus isolates and hosts can be given for one evaluation. The function of the program MINDIF is based on computation of all values of P_{kl}, all values of R_i and sorting pairs of virus isolates according to increasing P_{kl} values. The input data are the number

Fig. 6

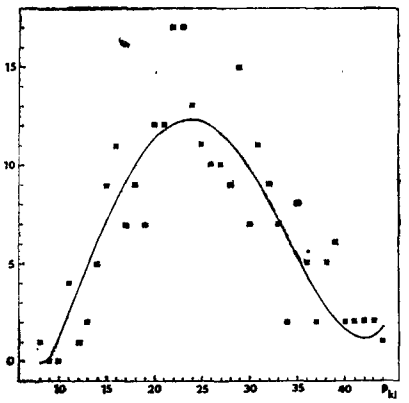


Fig. 7

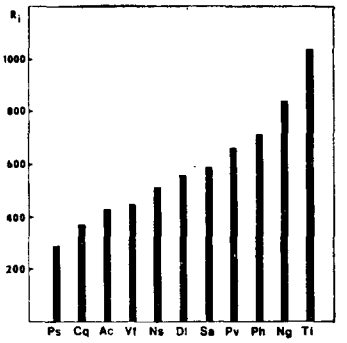


Fig. 6. Distribution of differences between isolates (P_{kl} values) derived from sorting isolate pairs. The curve (fitting polynomial approximation in the least square sense) corresponds to real values ($P < 0.01$).
Fig. 7. Quantitative evaluation of host fitness in accordance with isolate differentiation. (Names of host plants abbreviated as in Table 2.)

of isolates given by a definite form, the number of hosts and the values of V_{ji} and C_{ji} for all i and for all j ($i = 1, 2, \ldots, n$, $j = 1, 2, \ldots, m$).

The output of the program MINDIF represents printing of (1) the given input data, (2) the table of P_{kl} values, (3) all pairs of isolates sorted by increasing values of P_{kl} and (4) the R_i values for all hosts.

RESULTS

Electron microscopy readily revealed elongated virus particles with all isolates excepting the isolate 8 (Kralupy 1). Enormous amounts of virus particles were observed with the isolate 6 (Hodkovičky 2).

Serological double-diffusion tests showed as early as within 19 h prominent specific straight bands of precipitation typical of low molecular-wt antigens between central serum wells and depots which contained infective sap with all TuMV isolates. No reactions were stated with control suspensions from healthy petunia plants and an unrelated Potyvirus isolated from *Wisteria sinensis* (Sims) Sweet, and with systems treated with normal serum. Specific serological reaction was also obtained with a TuMV isolate from horse-radish. Figs. 3, 4 and 5 demonstrate less distinct bands with some antigens in comparison with the homologous antigen (17). A weaker precipitation resulted with the isolate 13 (Lovosice 2), the isolate "Štětí 2" (not included into computer evaluation) and the previously determined TuMV isolate from horse-radish (specimen taken from horse-radish leaves).

TABLE 1
The source program MINDIF. (Translation of Czech expressions: zadané hodnoty vnímavosti a citlivosti — given values of susceptibility and sensitivity, výpočet minimálních diferencí — compute of minimum differences, tabulka diferencí — table of differences, seřazení diferencí podle velikosti — sorting differences according to their values, seřazení kmenů podle podobnosti — sorting strains according to similarity, určení vhodnosti hostitelů — ascertaining of host fitness, kvantitativní vyjádření vhodnosti hostitelů — quantitative evaluation of host fitness, chyba v řádu matice — error in the matrix range)

```
'BEGIN 'COMMENT 'USEFILE 30,41 ;
   'INTEGER M,N ;
   'INTEGER 'ARRAY REP[1:2] ;
   READ(41,REP) ;
   N:=REP[1] ;
   M:=REP[2] ;
   'IF M 'LE 0 'OR N 'LE 0 'THEN 'GOTO CHYBA ;
'BEGIN
   'BOOLEAN BOOL ;
   'INTEGER I,J,K,L,O ,RL;
   'INTEGER 'ARRAY A[1:M,1:N], B[1:M-1,2:M], C[1:(N-1)//2] ;
   READ(41,A) ;
   'IF N 'GE 30 'THEN 'GOTO NE ;
   WRITE(30,(:'**** ZADANE HODNOTY VNIMAVOSTI A CITLIVOSTI ****'///:)) ;
   WRITE(30,REP,(:((X1D3)R/)R:),A) ;
NE:    'FOR I:=1 'STEP 1 'UNTIL M-1 'DO
       'FOR J:=2 'STEP 1 'UNTIL M 'DO B[I,J]:=0 ;
      'FOR I:=1 'STEP 1 'UNTIL (N-1)//2 'DO C[I]:=0 ;
'COMMENT*****************************************************
        *
        *  VYPOCET MINIMALNICH DIFERENCI
        *
        *****************************************************;
  'FOR I:=1 'STEP 1 'UNTIL M-1 'DO
       'FOR J:=I+1 'STEP 1 'UNTIL M 'DO
           'FOR K:=2 'STEP 1 'UNTIL N 'DO B[I,J]:=B[I,J]+
                                          ABS(A[I,K]-A[J,K]) ;
   'IF M-1 'GT 24 'THEN 'GOTO NO ;
   REP[1]:=REP[2]:=M-1 ;
   WRITE(30,REP,(:P'**** TABULKA DIFERENCI ****'///
                 ((X1D4)R/)R:),B) ;
'COMMENT*****************************************************
        *
        *  SERAZENI DIFERENCI PODLE VELIKOSTI
        *
        *****************************************************;
NO:   WRITE(30,(:P'**** SERAZENI KMENU PODLE PODOBNOSTI ****'///:)):
   O:=0 ;
ZNOVA: RL:=30000 ;
   BOOL:='TRUE ;
   'FOR I:=1 'STEP 1 'UNTIL M-1 'DO
       'FOR J:=I+1 'STEP 1 'UNTIL M 'DO
           'BEGIN 'IF B[I,J] 'GE 0 'THEN
                 'BEGIN 'IF B[I,J] 'LE RL 'THEN
                        'BEGIN RL:=B[I,J] ;
                               K:=I ; L:=J ;
                               BOOL:='FALSE ;
                        'END ;
                 'END ;
           'END ;
   'IF BOOL 'THEN 'GOTO KONEC ;
   O:=O+1;
   B[K,L]:=-1 ;
   WRITE(30,(:D5X10D5X3D5X5D10/:),O,K,L,RL) ;
   'GOTO ZNOVA ;
'COMMENT*****************************************************
        *
        *  URCENI VHODNOSTI HOSTITELU
        *
        *****************************************************;
KONEC:  'FOR I:=1 'STEP 1 'UNTIL (N-1)//2 'DO
           'BEGIN 'FOR J:=1 'STEP 1 'UNTIL M-1  'DO
                     'FOR K:=J+1 'STEP 1 'UNTIL M 'DO
                       C[I]:=C[I]+ABS(A[K,2*I]-A[J,2*I])+
                                  ABS(A[K,2*I+1]-A[J,2*I+1])
           'END ;
   REP[1]:=(N-1)//2 ;
   WRITE(30,(:P'**** KVANTITATIVNI VYJADRENI VHODNOSTI HOSTITELU ****'//
/:)) ;
   WRITE(30,REP,(:(X2D6/)R:),C) ;
   'END ;
   'GOTO  END ;
CHYBA:  WRITE(30,(:'CHYBA V ŘADU MATICE':)) ;
END: 'END
```

TABLE 2

Given values of susceptibility (first cipher) and sensitivity (second cipher) for each of eleven differential hosts (abbreviated by initials) and for each of 23 TuMV isolates

TuMV isolates	Differential hosts										
	1 Pv	2 Vf	3 Ti	4 Ph	5 Ns	6 Sa	7 Ac	8 Ng	9 Di	10 Ps	11 Cq
1 (Benešov)	00	13	25	54	43	55	22	54	55	00	54
2 (Brandýs 1)	00	00	32	54	53	53	32	55	35	00	53
3 (Brandýs 2)	13	13	24	54	54	33	11	54	55	00	53
4 (Děčín 1)	00	12	00	13	33	53	33	53	14	00	43
5 (Děčín 2)	23	12	15	44	53	33	32	53	15	11	53
6 (Hodkovičky)	00	00	15	55	53	44	43	55	45	00	55
7 (Kolín)	23	12	14	54	54	54	32	55	55	00	54
8 (Kralupy 1)	11	00	00	11	31	54	42	22	23	11	53
9 (Kralupy 2)	12	00	41	22	31	23	43	21	23	11	53
10 (Litoměřice 1)	13	00	54	44	42	54	22	21	35	00	54
11 (Litoměřice 2)	11	00	55	13	33	34	32	22	24	00	32
12 (Lovosice 1)	22	12	43	34	54	22	32	54	55	00	43
13 (Lovosice 2)	12	13	23	55	55	53	32	54	55	11	53
14 (Lysá n. Lab.)	33	12	32	32	32	34	42	00	33	00	54
15 (Mělník 1)	22	00	13	14	54	54	22	32	55	00	55
16 (Mělník 2)	22	11	51	34	54	43	22	55	55	00	54
17 (Pardubice 1)	33	13	25	45	45	34	53	55	55	11	55
18 (Pardubice 2)	33	00	41	45	52	23	43	55	55	00	54
19 (Pardubice 4)	33	12	00	13	54	44	32	54	45	00	53
20 (Práče)	13	12	25	54	53	32	12	13	25	00	32
21 (Rokytka)	42	12	45	54	53	15	22	32	45	21	54
22 (Štětí 1)	42	11	55	34	53	55	33	53	55	22	54
23 (Zbraslav)	13	11	34	54	54	44	12	53	55	00	52

Hosts: 1 — *Phaseolus vulgaris* L. cv. Prince, 2 — *Vicia faba* L., 3 — *Trifolium incarnatum* L., 4 — *Petunia hybrida* hort. ex VILM., 5 — *Nicotiana sylvestris* SPEG. et COMES, 6 — *Sinapis alba* L., 7 — *Amaranthus caudatus* L., 8 — *Nicotiana glutinosa* L., 9 — *Datura innoxia* MILL., 10 — *Pisum sativum* L., 11 — *Chenopodium quinoa* WILLD.

Unequal serological reactions might be due to various virus concentrations in petunia plants, as suggested from the results of local lesion assay [the isolate 11 (Litoměřice 2) was also included because in one case a weaker serological reaction was also observed]. Numbers of local necrotic lesions on Samsun tobacco per 10 cm² of leaf blade:

17 (Pardubice 1) 62.2
11 (Litoměřice 2) 58.9
13 (Lovosice 2) 39.8
Štětí 2 . . . . . 15.2

The distinctness of precipitation bands was apparently influenced by virus concentration in saps. (Uniform plants were used for the above tests, for rubbing only the largest and two next elder leaves below were left, so that factors reducing or enhancing the lesion number by age and position of leaves could not misrepresent the results. If the largest leaf showed a definite number of lesions, the next leaf below showed $\times 1.32$ more lesions and the next one $\times 1.76$ more lesions.)

Serologically all isolates from *S. loeselii* were proved to be TuMV and to be related to a TuMV isolate from horse-radish.

TABLE 3
Differences (P_{kl}) between TuMV isolates

	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
1	16	14	26	22	15	13	39	43	23	32	22	15	35	23	21	21	29	26	24	22	21	16
2	.	20	22	22	13	17	31	31	21	28	20	17	33	23	17	31	19	24	26	30	27	18
3	.	.	32	16	23	11	43	39	25	34	14	11	33	23	17	19	23	20	16	24	27	8
4	.	.	.	24	29	29	21	29	35	26	28	29	33	29	29	39	35	18	32	42	35	32
5	.	.	.	.	23	15	33	31	25	28	18	17	29	25	23	19	25	20	16	20	21	18
6	.	.	.	.	.	16	36	38	26	31	27	22	38	22	24	20	20	27	29	29	26	21
7	.	.	.	.	.	.	38	42	22	35	15	12	30	16	14	16	20	15	23	23	20	11
8	.	.	.	.	.	.	.	14	28	23	41	36	26	26	38	44	38	27	39	41	40	39
9	.	.	.	.	.	.	.	.	24	21	31	36	20	32	32	40	26	35	35	33	36	37
10	.	.	.	.	.	.	.	.	.	19	27	28	22	18	22	32	24	31	23	23	24	19
11	.	.	.	.	.	.	.	.	.	.	28	37	27	25	31	39	35	32	22	30	31	28
12	.	.	.	.	.	.	.	.	.	.	.	15	29	21	11	23	17	18	22	22	21	16
13	.	.	.	.	.	.	.	.	.	.	.	.	36	22	18	16	24	21	25	25	22	15
14	.	.	.	.	.	.	.	.	.	.	.	.	.	30	30	32	28	27	29	29	34	31
15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18	28	26	19	29	25	24	19
16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24	14	17	29	25	18	15
17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	25	31	25	22	23
18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23	33	27	24	23
19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	30	27	20
20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24	33	16
21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	22
22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21

The similarity of TuMV isolates according to host reactions was compared with a computer by means of the source program MINDIF (Table 1), Table 2 contains the given values of susceptibility and sensitivity.

Differences between isolates were printed in Table 3. Sorting 253 pairs of TuMV isolates according to increasing P_{kl} values (8 to 44, modal values 22 and 23) was summarized in Fig. 6 showing distribution of differences and the character of the variability of TuMV isolates.

Investigating the fitness of hosts, as being more or less able to differentiate isolates of the given set from each other, proved *T. incarnatum* to be the best host ($R_i = 1034$) and *P. sativum* the worst one ($R_i = 288$). Fig. 7 implies that a larger set of hosts would demonstrate a better assorted curve. Nevertheless, some hosts having a high susceptibility (*e.g. N. sylvestris*) show differences especially in sensitivity (*e.g.* minute or large local lesions and their unequal growth); thus their importance as strain differentiating hosts is lowered by their high susceptibility to our evaluation method, as is also the case with *C. quinoa*.

DISCUSSION

The computer aided evaluation of relations of TuMV isolates is valid only for the given sets of isolates and hosts; both exert an influence upon the evaluating of more or less fitted hosts to differentiate TuMV strains. The role of the only spontaneous host *S. loeselii* could be judged after comparison with another set of isolates obtained from other natural hosts by means of the described method which is of general validity.

The only species (petunia) used as an infection source for inoculating differential hosts could exert a misleading influence esp. in the sense that

petunia plants were not able to propagate equally all TuMV isolates, as demonstrated with four isolates and also by electron microscopy of diluted leaf extracts.

TuMV isolates originating from *S. loeselii* plants in the same or a nearby locality might differ each other more than from isolates collected at very distant localities. Differences between groups of isolates originating from river basins of the Vltava or Labe before the confluence of both were similar to differences within individual groups. Thus, no geographical indicators could be established that would be useful for attempts to say anything about the isolate provenance.

The serological procedure used could only prove all isolates to be TuMV. However, it was not suitable for investigating differences between antigens; other methods would have to be applied for this purpose. (For one double diffusion test undiluted antiserum and antigens without pyrrolidine were used. Only sixteen isolates were compared with the homologous isolate 17 and a further eight isolate pairs with each other. Spurs indicated serological differences between the isolate 17 and the isolates 13, 18 and 23, between 7 and 18 and between 13 and 23. Unfortunately, this investigation was not completed.)

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Figs. 1, 2 at the end of the issue.

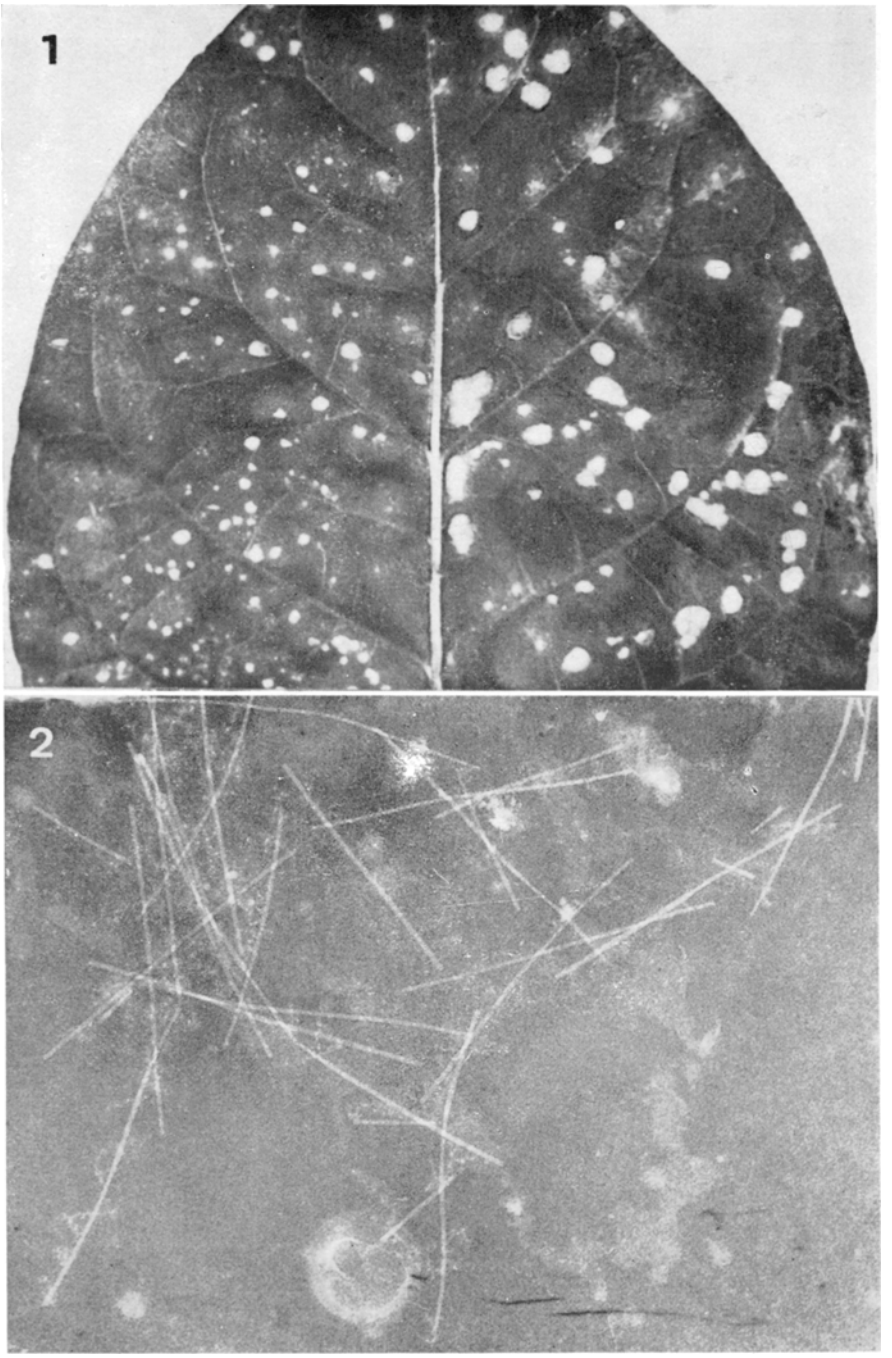

Fig. 1. Different local lesion reactions to isolates 20 — Práče (left) and 17 — Pardubice 1 (right) of a Samsun tobacco leaf six days after inoculation ($\times$ 1.5).
Fig. 2. Electron micrograph of diluted purified preparation of the isolate 17 (Pardubice 1), showing individual virus particles and a few fragments or end-to-end aggregates. Negatively stained with potassium phosphotungstate, $\times$ 59 000.