EXPERIMENTAL HOST RANGE OF THE POTATO SPINDLE TUBER 'VIRUS'

R. P. Singh[1]

Abstract

Two hundred thirty-two plant selections (species and varieties) were tested for susceptibility to the potato spindle tuber 'virus' (PSTV). One hundred thirty-eight selections were found to be susceptible to PSTV but no 'virus' was recovered from the remaining 94. Susceptible plants were found in the families Boraginaceae, Campanulaceae, Caryophyllaceae, Compositae, Convolvulaceae, Dipsaceae, Sapindaceae, Scrophulariaceae, Solanaceae, and Valerianaceae. Most of the susceptible selections were symptomless carriers of PSTV. Visible symptoms were produced by both mild and severe strains of PSTV in *Lycopersicon esculentum* cv. Allerfruheste-frëiland, *Scopolia anomala, S. corniolica, S. lurida, S. sinensis, S. stramonifolia, S. tangutica, Solanum aviculare,* and *S. avicular* var. *albiforme*; and only by the severe strain in *Gynura aurantica, Petunia hybrida* var. Burpee Blue, and *Solanum depilatum.* Temperature of 21.1 - 22.8 C (70-73 F) with a light intensity of about 400 ft-c favored local lesion development in *Scopolia sinensis. S. sinensis* appeared to be more susceptible than other *Scopolia* species.

Introduction

The first attempt to transmit the potato spindle tuber virus (PSTV) to plants other than potato was by Goss (5). He met with no success. Almost 30 years later MacLachlan (11) screened 188 plant species in 18 genera for susceptibility to several isolates of PSTV. But again no symptoms, local or systemic, attributable to PSTV alone developed in any of the test plants. The first plant used successfully as an indicator for PSTV was tomato (*Lycopersicon esculentum* Mill. cv. Rutgers) by Raymer and O'Brien (14). This finding was soon followed by reports that other plants were susceptible to PSTV (2, 13, 20).

The difficulty encountered in earlier searches was explained by Fernow's (3) results, when he demonstrated that there were mild strains of PSTV which produced practically no symptoms on plants of tomato varieties then in use. Raymer and O'Brien (14) had been fortunate enough to have chosen a severe strain of PSTV from the Schultz virus collection. Searches for improved indicator plants continued and although some progress was reported by O'Brien (12) and Singh and O'Brien (22), a local lesion host was not found until 1971 (18).

The field surveys indicating prevalence of mild strains (23) and the desirability of indexing the potato seedlings for seed transmitted PSTV (4, 7, 17) stressed the need for diagnosis of the mild strains. Some of the results obtained at earlier stages of the present investigation have been published (16, 18). Here I present the reactions of 232 plant species and varieties (selections) to PSTV, describe additional local lesion hosts, and report on the environmental conditions favoring lesion production.

[1]Research Scientist, Canada Department of Agriculture, Research Station, Fredericton, New Brunswick. Received for publication July 27, 1972.

Materials and Methods

Seeds of different plant selections were obtained from W. J. Cody, Phanerogamic Herbarium, Plant Research Institute, Ottawa, Canada. Seeds were germinated in a peat-vermiculite mix and the resulting seedlings were transplanted to a soil mix in 15 cm clay pots. Vigorously growing, uniform plants bearing three to four leaves were used in the inoculation tests. Leaves of six plants from each species were inoculated with each strain. All the tests were repeated at least twice.

Mild (Fernow ii) and severe (from Schultz collection) strains of PSTV, used in previous studies (19, 20, 23) were maintained in potato (*Solanum tuberosum* L. cv. Saco) plants. Inoculum, unless stated otherwise, consisted of a crude ribonucleic acid preparation from PSTV-infected potato leaves, as described earlier (19). The ribonucleic acid preparations were applied with Q-tips (Chesebrough-Pond's (Canada) Limited, Markham, Ontario) on the leaves of test plants, previously dusted with 350-mesh carborundum. Inoculated leaves were rinsed with tap water. Several tomato plants were inoculated with the severe strain of PSTV and placed among the test plants as controls for symptom development.

Initially, inoculated plants were maintained in the greenhouse at 27-31 C under an 18-hr day with light intensities ranging from 600-800 ft-c provided by fluorescent, incandescent or mercury bulbs. Later, environmental conditions were varied as stated under results section. Plants were observed for up to a month for visible symptoms. A composite leaf sample from the inoculated plants of each species was indexed on Sheyenne tomato for recovery of PSTV. Readings for the severe strain of PSTV were made directly. The mild strains of PSTV were indexed by means of Fernow's cross-protection (3) test.

Results

Two hundred thirty-two plant selections (species and varieties) from 36 families were screened for susceptibility to PSTV. More than half of the selections, representing 23 genera, were from the family Solanaceae. Plants susceptible to PSTV were found in families Boraginaceae, Campanulaceae, Caryophyllaceae, Compositae, Convolvulaceae, Dipsaceae, Sapindaceae, Scrophulariaceae, Solanaceae, and Valerianaceae (Table 1). Of 138 susceptible selections only 12 from the families Compositae and Solanaceae devloped visible symptoms. One hundred twenty-six selections were symptomless carriers (Table 1), and the remaining 94 selections developed no symptoms, nor could PSTV be recovered by sub-inoculation to tomato (Table 2). Since host susceptibility was essentially similar with both the mild and severe strains, the plant species are grouped on the basis of susceptibility to both strains. Exceptions are described separately.

Plant species with visible symptoms:

Gynura aurantica DC. About 30-40 days after inoculation with severe strain, the new leaves were reduced in size, curled inward and had dark veinal spotting. The entire top growth was clustered together and infected plants were severely stunted (Fig. 1). Symptom development was pronounced at a temperature of 28-31 C. and at a lower temperature of 20-24 C infected plants were symptomless carriers of PSTV.

TABLE 1.—*Symptomless plant selections, susceptible to mild and severe strains of potato spindle tuber virus.*

Family and species
Boraginaceae
Myosotis sylvatica Hoffm.
Campanulaceae
Campanula medium L.
Caryophyllaceae
Cerastium tomentosum L.
Dianthus barbatus L.
Convolvulaceae
Convolvulus tricolor L.
Dipsaceae
Scabiosa japonica Miq.
Sapindaceae
Cordiospermum halicacabum L.
Scrophulariaceae
Penstemon richardsonii Dougl.
Solanaceae
Atropa belladonna L.
Browallia demissa L.
Browallia grandiflora Grah.
Browallia viscosa H.B.K.
Capsicum microcarpum DC.
Capsicum nigrum Willd.
Cyphomandra betacea Sendtn.
Lycopersicon esculentum Mill. var. *cerasiforme* Dun.
Lycopersicon esculentum Mill. var. *racemiforme* Lange
Lycopersicon esculentum Mill. var. *cordiforme*
Lycopersicon esculentum Mill. var. *pyriforme* Dun.
Lycopersicon esculentum Mill. cv. Ace
Lycopersicon esculentum Mill. cv. Alice Roosevelt
Lycopersicon pimpinellifolium Mill.
Nicotiana alata Link & Otto
Nicotiana bigelovii Wats.
Nicotiana bonariensis Lehm.
Nicotiana chinensis Fisch.
Nicotiana clevelandii Gray.

Family and species
Solanaceae
Nicotiana glauca Grah
Nicotiana goodspeedii Wheeler
Nicotana clevelandii x Nicotiana glutinosa Christie
Nicotiana knightiana Goodspeed.
Nicotiana langsdorffii Weinm.
Nicotiana longiflora Cav.
Nicotiana megalosiphon Heurck & Meull.
Nicotiana nudicaulis Wats.
Nicotiana paniculata L.
Nicotiana plumbaginifolia Viv.
Nicotiana quadrivalvis Pursh
Nicotiana raimondii Macbride
Nicotiana repanda Willd.
Nicotiana rotundifolia Lindl.
Nicotiana sanderae Hort.
Nicotiana solanifolia Walp.
Nicotiana silvestris Speg. & Comes
Nicotiana texana Hort.
Nicotiana viscosa Lehm.
Nierembergia coerulea Gill.
Petunia axillaris BSP.
Petunia inflata Fries
Petunia nyctaginiflora Juss.
Petunia violacea Lindl.
Physalis alkekengi L.
Physalis angulata L.
Physalis edulis Sims
Physalis francheti Mast.
Physalis heterophylla Nees
Physalis ixocarpa Brot.
Physalis minima L.
Physalis parviflora Hort.
Physalis philadelphica Lam.
Physalis pruinosa L.
Physalis pubescens L.

TABLE 1.—*(Continued)*

Family and species
Solanaceae
Physalis somnifera L.
Physalis viscosa L.
Pyrracanthum villisum Lam.
Pyrracanthum sysimbrifilium Lam.
Salpiglossis sinuata Ruiz. & Pav.
Salpiglossis variabilis Hort.
Salpiglossis spinescens Clos. var. Mixed hybrids
Saracha jaltomata Schlecht.
Saracha umbellata D.C.
Schizanthus pinnatus Ruiz. & Pav.
Schizanthus retuses Hook.
Scopolia physaloides Dun.
Solanum aethiopicum L.
Solanum alatum Moench
Solanum americanum Mill.
Solanum atriplicifolium Gill.
Solanum auriculatum Ait.
Solanum bonariense L.
Solanum capsicastrum Link.
Solanum carolinense L.
Solanum cervantesii Lag.
Solanum chlorocarpum Schur.
Solanum ciliatum Lam.
Solanum cornutum Lam.
Solanum decipiens Opiz.
Solanum diflorum Vellozo
Solanum dulcamara L.
Solanum gracile Otto
Solanum guineense L.
Solanum hendersonii Hort.
Solanum hibiscifolium Rusby
Solanum humile Bernh.
Solanum humistratum Rshw.
Solanaceae
Solanum judaicum Bess.
Solanum kitaibeli Schult.
Solanum laciniatum Ait.
Solanum luteum Mill.
Solanum macroglobularum Rshaw.
Solanum maritimum Megen
Solanum melongena L.
Solanum memphiticum Gmel.
Solanum miniatum Bernh.
Solanum nigrum L.
Solanum nitidibaccatum Bitt.
Solanum nodiflorum Jacq.
Solanum ochroleucum Bast.
Solanum olgae Pojark.
Solanum ottonis Hyl.
Solanum papita Rydb.
Solanum paranense Dusen
Solanum persicum Willd.
Solanum pseudocapsicum L.
Solanum pyracanthum Jacq.
Solanum rantonnetti Carr.
Solanum saponaceum Dun.
Solanum sinaicum Boiss.
Solanum sisymbrifolium Lam.
Solanum sodomeum L.
Solanum surrattense Burm.
Solanum tomentosum L.
Solanum tripartitum Dun.
Solanum umbellatum Mill.
Solanum verbascifolium L.
Valerianaceae
Valeriana officinalis L.

FIG. 1.—Potato spindle tuber virus in *Gynura aurantica*. Right — healthy plant, left — infected plant.

TABLE 2.—*Plant selections resistant to both mild and severe strains of potato spindle tuber virus.*

Family and species
Aizoaceae
Tetragonia expansa Murr.
Amaranthaceae
Amaranthus albus L.
Amaranthus retroflexus L.
Gomphrena globosa L.
Begoniaceae
Begonia semperflorens Link & Otto
Berberidaceae
Podophyllum hexandrum Royle
Bigoniaceae
Incarvillea delavayi Bur. & Franch.
Boraginaceae
Borago officinalis L.
Cynoglossum amabile Stapf & Drummond
Capparidaceae
Cleome spinosa L.
Polanisia trachysperma Torr & Gray
Chenopodiaceae
Atriplex gmelini Mey.
Atriplex hortensis L.
Atriplex littoralis L.
Chenopodium album L.
Chenopodium amaranticolor Coste & Reyn.
Chenopodium capitatum Aschers.
Chenopodium strictum Roth
Compositae
Cichorium endivia L.
Lactuca sativa L.
Cruciferae
Brassica botrytis Mill.
Brassica capitata Hort.
Brassica rapa L.
Cucurbitaceae
Bryonia alba L.

Family and species
Cucurbitaceae
Citrullus vulgaris Schrad.
Cucumis anguria L.
Cucumis myriocarpus Naud.
Euphorbiaceae
Ricinus communis L.
Geraniaceae
Geranuium sanguineum L.
Hydrophyllaceae
Nemophila insignis Benth.
Phacelia campanularia Gray
Labiatae
Coleus blumei Benth.
Physostegia virginiana Benth.
Leguminosae
Glycine max Merrill
Lathyrus odoratus L.
Phaseolus vulgaris L. cv. Greenpod
Phaseolus vulgaris L. cv. Blue Lake
Pisum sativum L. cv. Perfection
Pisum sativum L. cv. Jet
Trigonella foenum-graceum L.
Liliaceae
Kniphofia uvaria Th. Dur. & Schinz
Malvaceae
Hibiscus esculentus L.
Hibiscus manihot L.
Lavatera trimestris L.
Onagraceae
Clarkia elegans Dougl.
Godetia amoena Don
Papaveraceae
Eschscholzia californica Cham.
Papaver orientale L.
Phytolaccaceae
Phytolacca decandra L.

TABLE 2.—(*Continued*)

Family and species
Plumbaginaceae
Limonium sinuatum Mill.
Polygonaceae
Rheum rhaponticum L.
Portulacaceae
Portulaca grandiflora Hook.
Rubiaceae
Asperula odorata L.
Scrophulariaceae
Pentstemon hartwegii Benth.
Pentstemon hirsutus Willd.
Solanaceae
Capsicum chacoense Hunziker
Capsicum grossum Willd.
Cestrum elegans Schlecht.
Cestrum euanthes Schlecht.
Cestrum nocturnum L.
Cestrum tomentosum L.
Datura aegyptica Vesl.
Datura arborea L.
Datura ceratocaula Jacq.
Datura chlorantha Hook.
Datura ferox Nees.
Datura inoxia Mill.
Datura leichhardtii Muell.
Datura meteloides DC.
Datura quercifolia H.B.K.
Datura sanguinea Ruiz. & Pav.
Solanaceae
Datura sarmentosa Lam.
Datura stramonium var. *inermis* Jacq.
Datura stramonium var. *tatula* L.
Datura wrightii Hort.
Hyoscyamus albus L.
Hyoscyamus niger L.
Indigofera gerardiana Grah.
Lycium barbarum L.
Lycium chinense Mill.
Lycium europaeum L.
Lycium halimifolium Mill.
Lycium mediterraneum Dun.
Solandra hirsuta Dun.
Solanum hetrodoxum Dun.
Vestia lycioides Willd.
Withania somnifera Dun.
Umbelliferae
Coriandrum sativum L.
Foeniculum vulgare Mill.
Thymus vulgaris L.
Pimpinella anisum L.
Apium graveolens L.
Verbenaceae
Lantana camara L.
Violaceae
Viola cornuta L.

Petunia hybrida Vilm. cv. 'Burpee Blue'. About 4-5 weeks after inoculation with severe strain of PSTV, the undersides of leaf mid-veins and main lateral veins developed necrosis (Fig. 3A). In later stages, leaves developed a crinkled appearance. The plants were moderately stunted and bushy from the development of an abnormal number of secondary shoots. *Petunia* plants remained symptomless with mild strain of PSTV.

Scopolia species. About 8-11 days after inoculation, necrotic local lesions almost circular in shape developed on leaves of *S. anomala* (Link et. Otto) Airy-Schaw., *S. corniolica* Jacq., *S. lurida* Dun., *S. sinensis* Hemsl., and *S. stramonifolia* (Wall.) Semenova, whereas 18-22 days were required for lesions on *S. tangutica* Maxim. The lesions increased in size with age, approaching to 2-3 mm on *S. anomala*, *S. corniolica* and *S. lurida* (Fig. 2A) species, while remaining about 1 mm on *sinensis* (Fig. 2B). The lesions on *S. stramonifolia* were about 1-2 mm, but in addition there were several brown longitudinal streaks on the veins (Fig. 2C). On *S. tangutica* local lesions were few in numbers, but of larger size (Fig. 2D), later developing into blotchy spots. The systemic necrotic spotting developed about 5-7 days after the appearance of local lesions in most species except in *S. sinensis*, in which they developed after 10-15 days. Systemic symptoms were similar in all the *Scopolia* species, consisting of a network of necrotic veins and necrotic spots of various sizes, followed by chlorosis of the entire leaf (Fig. 3C). Eventually leaves became brown and dropped off, leaving bare stems and shoots (Fig. 3E). Necrotic discolorations were then evident on the stems. Symptoms in *Scopolia* species were similar with both mild and severe strains.

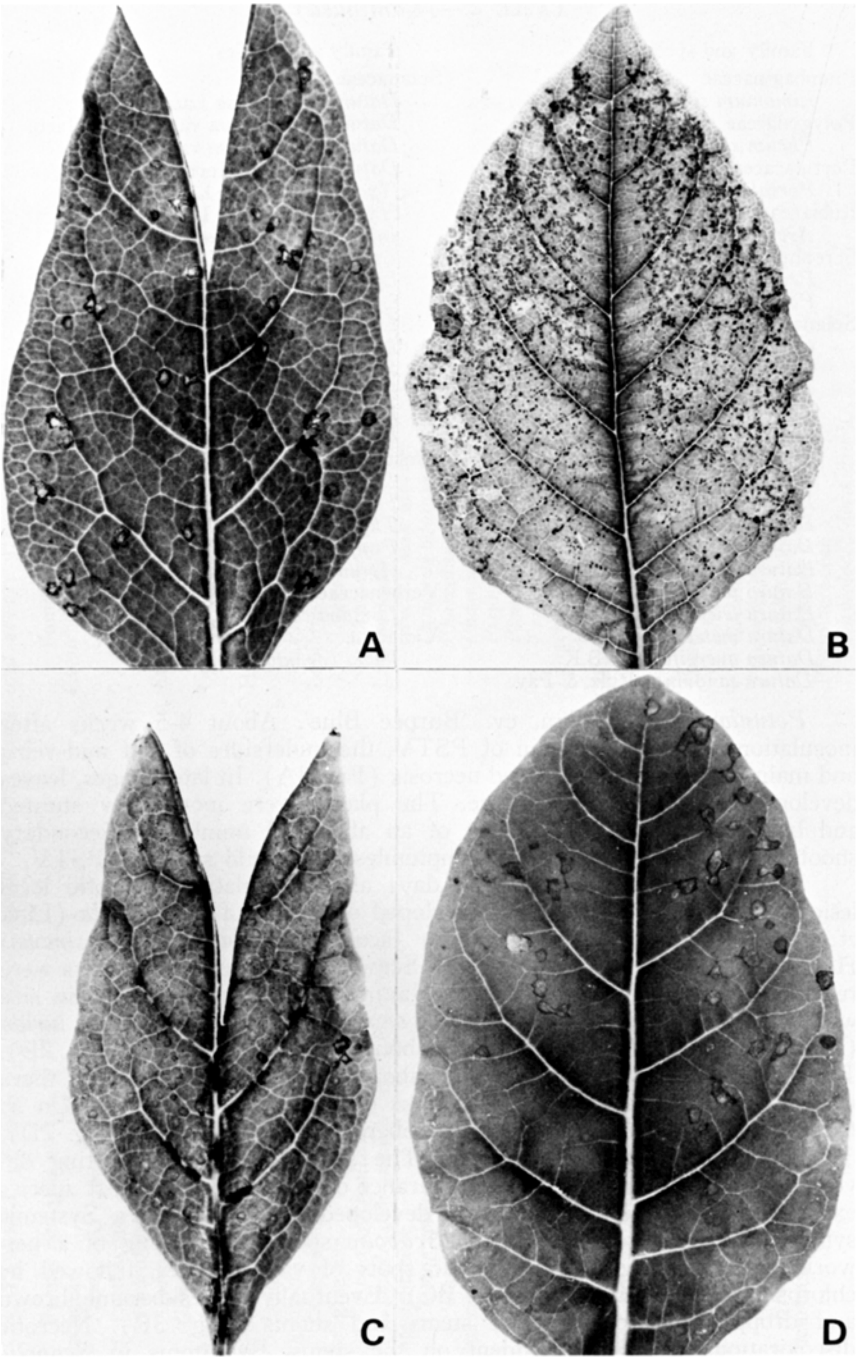

FIG. 2.—Local lesions produced by potato spindle tuber virus on various species of *Scopolia*: A) *S. lurida*, B) *S. sinensis*, C) *S. stramonifolia*, D) *S. tangutica*.

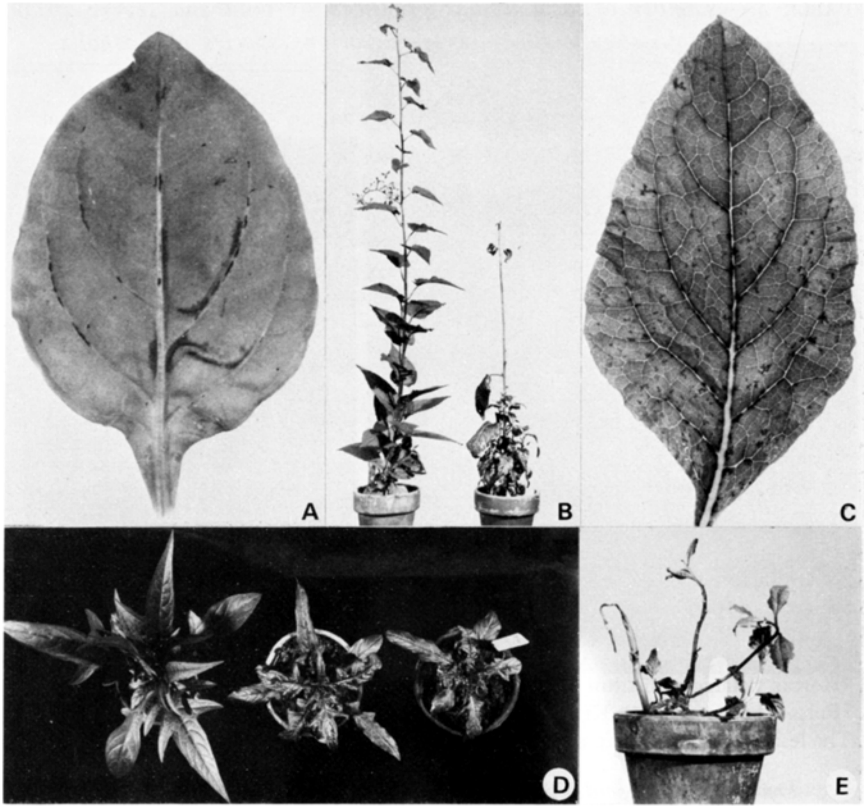

FIG. 3.—Symptoms produced by potato spindle tuber virus on different host plants: A) Brown discoloration on the underside of *Petunia* hybrid cv. 'Burpee Blue' leaf; B) Left healthy, right infected plant of *Solanum depilatum*; C) Systemic necrotic symptoms on *Scopolia sinensis*; D) Left healthy, middle mild strain, and right severe strain infected plants of *Solanum aviculare*; E) Plants of *Scopolia lurida* with bare stem, after infection with PSTM.

Solanum avicular Forst. and *S. avicular* Forst. var. *albiforme* Cheesem. In both species newly developing leaves were puckered and crinkled; progressively more reduced in size and closer together. Plants were more seriously stunted with the severe strain and less so with the mild (Fig. 3D). Later, leaves developed veinal necrosis, followed by chlorosis and leaf drop. Initial symptoms appeared in about 3-4 weeks.

Solanum depilatum Kitag. Three to four weeks after inoculation brown discoloration of the mid-veins was evident on the leaves; and numerous shoots began to develop from the leaf axil. Later, most of veins were necrotic. the leaves became chlorotic and dropped off, leaving the stem bare (Fig. 3B). Infected plants were severely stunted. Symptoms were produced only by the severe strain. The mild strain was carried symptomlessly.

TABLE 3.—*Number of local lesions produced by mild and severe strains of the potato spindle tuber virus in various species of Scopolia.*

	Mild strain		Severe strain	
	Duration (in days)	Lesion number	Duration (in days)	Lesion number
Scopolia anomala[1]	13	150	12	183
Scopolia lurida[2]	13	220	12	257
Scopolia lurida[3]	13	164	12	220
Scopolia lurida[4]	13	91	13	62
Scopolia corniolica[4]	13	116	12	148
Scopolia sinensis[4]	13	275	11	477
Scopolia sinensis[5]	—	0	—	0
Scopolia stramonifolia[5]	13	132	12	250
Scopolia stramonifolia[6]	13	116	12	189
Scopolia tangutica[5]	22	61	20	71
Scopolia tangutica[6]	22	60	20	72
Scopolia physaloides[7]	—	0	—	0

Seeds originally obtained from:
[1]University Botanical Garden, Cambridge, England.
[2,3]Jardin Botanique de la Ville, Rouen, France.
[4]Botanic Garden, Leiden, The Netherlands.
[5]Institutum Botanicum nom. V.L. Komarovii, Academiae Scientiarum, Leningrad, U.S.S.R.
[6]Hortus botanicus instituti plantarum officinalium, Vilar prov., Mosquensis, U.S.S.R.
[7]Polsa Akademia Naua, Krokow, Poland.
The lesion numbers are an average of eight half-leaves.

Lycopersicon esculentum cv. Allerfruheste-freiland. The symptoms of this cultivar of tomato have already been described (9). Briefly, they consisted of rugosity of leaves, veinal necrosis and severe stunting of plants. Veinal necrosis developed with both strains of PSTV.

Comparison of several species of Scopolia with regard to lesion production by the mild and severe strains of PSTV.

Six species of *Scopolia*, obtained from different sources, were compared for their reactions to PSTV. The test plants were used in the 4-5 leaf stage and the two uppermost fully developed leaves were inoculated with crude sap from PSTV infected Saco potato. A drop of appropriately diluted sap was spread on the leaf with a moist Q-tip. Plants were maintained under environmental conditions which were found to give optimum lesion production (see below).

The data from local lesion counts are presented in Table 3. There was no difference between mild and severe strains in symptom expression in these tests. *S. sinensis*, *S. lurida*, *S. stramonifolia*, and *S. corniolica*, in that order, developed the most lesions, and could be used for indexing. Of the species developing lesions, all except *S. tangutica* developed symptoms within 2 weeks.

The difference between two collections of *S. sinensis* was striking; the *S. sinensis* obtained from Leningrad U.S.S.R. failed to produce any symptoms, although PSTV was recovered from inoculated leaves. This

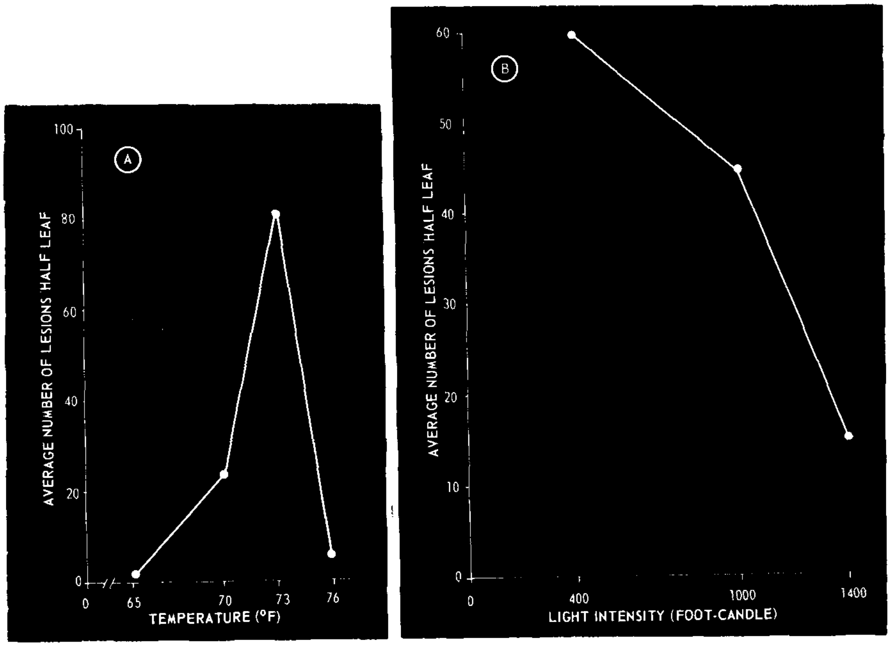

FIG. 4.—Effect of light and temperature on local lesion production in *Scopolia sinensis*: A) Effect of temperature; B) Effect of light intensity.

plant differs morphologically from *S. sinensis* received from the Netherlands (18). Also, in *S. lurida*, different collections showed differences in morphological characters as well as in lesion production. Another species, *S. physaloides*, was symptomless to both strains of PSTV.

Effect of temperature and light on the lesion production in Scopolia sinensis.

In a preliminary trial it was learned that local lesions on leaves of *S. sinensis* developed best at 22-23 C. Plants maintained at 28-31 C developed mostly systemic symptoms, without conspicuous local lesions. For a more critical determination of the effect of temperature, tests were conducted at four different temperatures (18.3 C, 65 F; 21.1 C, 70 F; 22.8 C, 73 F; 24.4 C, 76 F; photoperiod 18 hr at 400 ft-c, relative humidity about 70%). The results (Fig. 4A) are based on an average of the lesions per 30 half-leaves. The largest numbers of lesions were obtained at 22.8 C (73 F).

In another test, at 18 or 25 C, when plants with only a few lesions were transferred to 22.8 C, they developed numerous lesions within 3 days of the transfer.

Twenty inoculated half-leaves were tested under each of these light intensities, 400, 1000, and 1400 ft-c supplied by fluorescent and incandescent bulbs, about 2 feet above the plant level. The test was repeated three times. The lower light intensity of 400 ft-c favoured the lesion production (Fig. 4B).

Discussion

This study was initiated to find a local lesion or fast-reacting host plant, which could be used to diagnose both mild and severe strains of PSTV and which would facilitate quantitative estimations of PSTV concentration in purification studies. *Scopolia sinensis* clearly fulfills these objectives (18, 21). Further work on other species of *Scopolia*, including *S. sinensis* grown from seed of selected parents for use in potato-indexing for PSTV is in progress.

It was necessary to test plants other than those used in plant virus studies. The genus *Scopolia* has been neglected from host-range studies of plant virus (10, 25), although a species of *Scopolia* was used in a potato virus X host-range study in the early fifties (8). Since several species of *Scopolia* developed local lesions with PSTV and the citrus exocortis agent (24), but not with viruses like potato virus M, S, X, Y (18), and tobacco mosaic (unpublished data), it appears that this genus may be particularly suitable as test plant for viruses consisting of free-ribonucleic acid. The importance of seed source of *Scopolia* in such tests is significant. Striking variability was noted in the case of *S. sinensis* seed sources for their reaction of PSTV (Table 3). This type of variability in an indicator plant has been noted before by Bagnall et al. (1) in *Datura metel* L. where seed from only one of three seed lots tested responded with local lesions to potato virus M.

Potato spindle tuber virus has a much wider host-range than previously reported. Transmission and recovery of PSTV from several non-solanaceous plant species indicates that the virus can exist in hosts outside of the potato family. Whether the virus exists naturally in plants in other groups is not known. This possibility, in view of its pollen and seed transmissibility (4, 7, 17), should be explored to determine if there is a reservoir in off-season or overwintering plants.

PSTV local lesions in *Scopolia* species develop more uniformly under lower light intensity and temperature conditions than is required for symptom expression in tomato. At higher temperature, only systemic symptoms are produced in *Scopolia*. This situation is similar to potato virus X local lesions in *Datura metel* L. (15). Although the results presented in Fig. 4A, indicate a narow temperature range for effective lesion development in *Scopolia*, variation from this temperature within the range of 20-28 C for a few hours per day in the greenhouses did not retard lesion production seriously. However, temperatures of 25-30 C, and a light intensity above 600 ft-c for several days induced poor growth and thick leathery leaves that were less susceptible to infection (unpublished data).

The use of *Scopolia* as a local lesion host for PSTV is of considerable practical importance, in indexing of large numbers of potaoes for the presence of mild strains of PSTV. With a seed-producing technique available for *Scopolia sinensis* (6), the use of this species for routine potato indexing may become as simple as the use of *Gomphrena globosa* L. for potato virus X.

Acknowledgment

I am grateful to R. E. Finnie for excellent technical assistance and to B. A. Allen for some of the photographs.

Literature Cited

1. Bagnall, R. H., R. H. Larson and J. C. Walker. 1956. Potato viruses M, S, and X in relation to interveinal mosaic of the potato Irish Cobbler variety. Univ. Wisconsin Res. Bull. 198, 45 p.
2. Easton, G. D. and D. C. Merriam. 1963. Mechanical inoculation of the potato spindle tuber virus in the genus *Solanum*. (Abstr.) Phytopathology 53: 349.
3. Fernow, K. H. 1967. Tomato as a test plant for detecting mild strains of potato spindle tuber virus. Phytopathology 57: 1347-1352.
4. Fernow, K. H., L. C. Peterson and R. L. Plaisted. 1970. Spindle tuber virus in seeds and pollen of infected potato plants. Amer. Potato J. 47: 75-80.
5. Goss, R. W. 1931. Infection experiments with spindle tuber and unmottled curly dwarf of the potato. Nebraska Agr. Expt. Sta. Res. Bull. No. 53, 36 p.
6. Hanneman, Jr., R. E. and R. P. Singh. 1972. Seed production in the virus indicator plant, *Scopolia sinensis* Hemsley. Can. Plant Dis. Survey 52: 60-61.
7. Hunter, D. E., H. M. Darling and W. L. Beale. 1969. Seed transmission of of potato spindle tuber virus. Amer. Potato J. 46: 247-250.
8. Ladeburg, R. C., R. H. Larson and J. C. Walker. 1950. Origin, interrelation and properties of ringspot strains of virus X in American potato varieties. University Wisconsin Res. Bull. 165, 47 p.
9. Lee, C. R. and R. P. Singh. 1972. Enhancement of diagnostic symptoms of potato spindle tuber virus by manganese. Phytopathology 62: 516-520.
10. Macfarlane, Helen H. 1968. Review of applied mycology, plant host-pathogen index to volumes 1-40 (1922-1961). C.A.B. England 820 p.
11. MacLachlan, D. S. 1960. Potato spindle tuber in eastern Canada. Amer. Potato J. 47: 13-17.
12. O'Brien, Muriel J. 1972. Hosts of potato spindle tuber virus in suborder Solanineae. Amer. Potato J. 49: 70-72.
13. O'Brien, Muriel J. and W. B. Raymer. 1964. Symptomless hosts of the potato spindle tuber virus. Phytopathology 54: 1045-1047.
14. Raymer, W. B. and Muriel J. O'Brien. 1962. Transmission of potato spindle tuber virus to tomato. Amer. Potato J. 39: 401-408.
15. Singh, R. P. 1969. Use of *Datura metel* L. as a local lesion host for potato virus X. Amer. Potato J. 46: 355-357.
16. Singh, R. P. 1970. Occurrence, symptoms, and diagnostic hosts of strains of potato spindle tuber virus. (Abstr.) Phytopathology 60: 1314.
17. Singh, R. P. 1970. Seed transmission of potato spindle tuber virus in tomato and potato. Amer. Potato J. 47: 225-227.
18. Singh, R. P. 1971. A local lesion host for potato spindle tuber virus. Phytopathology 61: 1034-1035.
19. Singh, R. P. and R. H. Bagnall. 1968. Infectious nucleic acid from host tissues infected with the potato spindle tuber virus. Phytopathology 58: 696-699.
20. Singh, R. P. and R. H. Bagnall. 1968. *Solanum rostratum* Dunal., a new test plant for the potato spindle tuber virus. Amer. Potato J. 45: 335-336.
21. Singh, R. P. and M. C. Clark. 1971. Infectious low-molecular weight ribonucleic acid from tomato. Biochem. Biophys. Res. Comm. 44: 1077-1083.
22. Singh, R. P. and Muriel J. O'Brien. 1970. Additional indicator plants for potato spindle tuber virus. Amer. Potato J. 47: 367-371.
23. Singh, R. P., R. E. Finnie and R. H. Bagnall. 1970. Relative prevalence of mild and severe strains of potato spindle tuber virus in eastern Canada. Amer. Potato J. 47: 289-293.
24. Singh, R. P., M. C. Clark and L. G. Weathers. 1972. Similarity of host symptoms by citrus exocortis and potato spindle tuber causal agents. (Abstr.) Phytopathology 62: 790.
25. Thornberry, H. H. 1966. Plant pests of importance to North American agriculture — index of plant virus diseases. United States Department of Agriculture, Handbook No. 307, 446 p.