# Three strains of bean yellow mosaic virus: symptoms and accumulation in eight pea cultivars (*Pisum sativum* L.)

JARI P.T. VALKONEN

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A pea mosaic strain and a bean strain of bean yellow mosaic virus (BYMV) were isolated from naturally infected pea and broad bean plants and named BYMV-Ps and BYMV-Vf, respectively. A third strain of BYMV isolated from *Gladiolus* (BYMV-G) was obtained from Denmark which was distinguished from the two above strains serologically and by its symptoms in test plants.

BYMV-Ps and BYMV-Vf caused yellow mosaic symptoms and green mosaic symptoms, respectively, in eight pea cultivars tested, but the concentration of BYMV varied among the cultivars. BYMV-G caused mild mosaic or vein clearing in peas. A need to improve resistance to BYMV in the Finnish pea varieties was recognized.

Key words: BYMV, broad bean, virus resistance

## Introduction

Bean yellow mosaic potyvirus (BYMV) occurs worldwide and infects several economically important legumes, including peas (*Pisum sativum* L.), beans (*Phaseolus* spp.) and broad beans (*Vicia faba* L.) and non-leguminous plant species, such as those in the family Iridaceae and the genus *Fagus*. In legumes, BYMV is transmitted by several species of aphids in a non-persistent manner, and also experimentally in sap of infected plants (BOS 1970a, TAPIO 1970, COCKBAIN 1983, HAMPTON 1984, JAYASENA and RANDLES 1985, BAYS and DEMSKI 1986, WINTER and NIENHAUS 1989, PROVIDENTI 1991). Many strains of BYMV have been reported which may be distinguished by host range, aphid transmission, serology or RNA sequence heterology (BOS 1970a, JONES and DIACHUN 1977, REDDICK and BARNETT 1983, SCHMIDT and ZOBYWALSKI 1984, HERRERA and SEPULVEDA 1986, BARNETT et al. 1987, SCOTT et al. 1989, HOPPS and MCLAUGHLIN 1990). The pea strain of BYMV, formerly considered a distinct virus from the bean strain of BYMV and called pea mosaic virus (PMV), causes bright yellow mosaic symptoms, whereas the bean strain of BYMV causes green mosaic symptoms in pea leaves (BOS 1970b, TAPIO 1970). Both strains of BYMV infect broad beans inducing similar symptoms and cytoplasmic and nuclear inclusions (BOS 1969, TAPIO 1970, COCKBAIN 1983). The bean and pea strains of BYMV occur naturally in Finland, and these strains may cause a yield loss of up to 62% and 30%, respectively, in peas depending upon the age at which the plants are infected (TAPIO 1970). BYMV has been observed to infect broad bean in the field in Finland in the 1970s (A. Kurppa, pers. com.).

Pea breeding programmes in Finland have been successful in increasing the protein content of peas and developing high-yielding semileafless (afila-

pea) varieties. Several new afila-pea varieties have been released by the Anttila Plant Breeding Farm (APBF) (formerly Hankkija Plant Breeding Institute) during the last decade. Many of them are cultivated or included in official variety testing programmes in other countries, e.g. Sweden, Norway, Denmark, Canada and Estonia (KUJALA 1953, KIELPINSKI and BLIXT 1982, HOVINEN 1988, S. HOVINEN pers. com.). However, breeding for resistance to viruses was not particularly emphasized, and only resistance to pea seed-borne mosaic virus has been incorporated into a few breeding lines (HOVINEN 1990). Pea plants with yellow mosaic symptoms are commonly found in experimental fields of APBF (S. HOVINEN pers. com.). In the present study, two strains of BYMV were isolated from naturally infected pea and broad bean plants. Eight pea cultivars were inoculated with the above Finnish BYMV isolates and one Danish BYMV isolate. These cultivars included some of the recently released varieties of APBF as well as one old Finnish and two Dutch cultivars commonly grown in Finland. The objective was to determine whether any resistance to BYMV from foreign genetic materials had been incorporated into new pea varieties by breeders in addition to the characters being deliberately selected.

## Material and Methods

### Plants and growing conditions

The following pea cultivars released by APBF were included in the experiments: Helka (Proco x Hja 51221), afila-type, released in 1986; Hemmo (Maro x Kalle), leaflet-type, released in 1980; Hovi (Filby x Heikka), afila-type, released in 1989; Kalle (Torstai x Folger), leaflet-type, released in 1952; Pika (Proco x Tammi), afila-type, released in 1986; and Tammi (Simo x Usatyj 5), afila-type, released in 1984. The Dutch leaflet-type cv. Proco and afila-type cv. Solara widely grown in Finland were also included.

Experiments were done in a screenhouse and a glasshouse under natural daylight at the University of Helsinki, Viikki (60°13'N) during August — mid-September in 1992. Seeds were sown into a mixture of steam-sterilized peat and washed sand (10:1 v/v), and the plants were watered daily with a solution containing 0.1% NPK fertilizer (5-7-6). Plants in the screenhouse were sprayed weekly with dimethoate, and the glasshouse was fumigated weekly with nicotine to prevent any contamination by aphids. Daily means of the minimum and maximum temperatures were 10°C and 19°C in the screenhouse and 16°C and 28°C in the glasshouse.

### Viruses

To obtain isolates of BYMV, leaves of pea and broad bean plants showing yellow and green mosaic symptoms were sampled in the experimental fields of the Anttila Plant Breeding Farm (60°25'N) on July 28, 1992. Batches of c. 20 -100 plants with bright yellow mosaic symptoms were found scattered in many pea fields (Fig. 1), and all the samples from those plants reacted strongly when tested in DAS-ELISA with the two antisera available to BYMV. The virus isolate from the pea breeding line Hja 57839 which gave the highest ELISA absorbance values was selected for further studies and named BYMV-Ps. Similarly, the virus isolate from the broad bean breeding line Hja 62029A, which produced the highest ELISA absorbance values for BYMV, was used in further experiments and named BYMV-Vf. One isolate of BYMV obtained from *Gladiolus* in Denmark by Dr. N. Paludan (isolate DK-17-3-4: BOYE et al. 1990, ALBRECHTSEN et al. 1991) was kindly provided in freeze-dried leaves of *Nicotiana benthamiana* Domin. by Dr. M. Albrechtsen, Danish Research Center for Plant Protection, Lyngby, Denmark, and this is referred to as BYMV-G. BYMV-Ps and BYMV-G were maintained in the pea cv. Kalle, and BYMV-Vf was maintained in the broad bean cv. Ukko.

### Antisera

Polyclonal antibodies raised in rabbits against BYMV-G and alkaline phosphatase (AP) conjugated antibodies were kindly supplied by Dr. M.

Fig. 1. A pea plant (breeding line Hja 57839) naturally infected with BYMV-Ps collected from the experimental fields of APBF.

Albrechtsen, and were used in all serological tests. Rabbit polyclonal antibodies (ATCC PVAS-368 4-85) to BYMV (HAMMOND and HAMMOND 1989) were obtained from the American Type Culture Collection (ATCC), Rockville, USA, and conjugated with AP at our laboratory. The BYMV antibodies from M. Albrechtsen and ATCC were used in parallel ELISA tests for the detection of BYMV in the field samples.

### Inoculations

BYMV was sap-inoculated by grinding 1 g of BYMV-infected leaves in 5 ml of 0.001 M phosphate buffer, pH = 7.5, and rubbing the sap onto carborundum-dusted stipules of pea seedlings and leaves of the other test plant species when the plants were 10 days old. Four plants each of the eight pea varieties and test plant species were inoculated with each of the three virus isolates in two replicate experiments.

### Virus detection

BYMV was detected by double antibody sandwich enzyme-linked immunosorbent assay (DAS-ELISA) (CLARK 1981) and by immunosorbent electron microscopy (ISEM) (ROBERTS and HARRISON 1979). Stipules or leaves of the three uppermost knots of the pea plants and the uppermost fully-expanded leaves of the other test plant species were sampled in duplicate. Samples were weighed and ground in four volumes (w/v) of extraction buffer for DAS-ELISA and in nine volumes (w/v) of 0.06 M phosphate buffer, pH = 6.5, for ISEM. In DAS-ELISA, the absorbances were recorded at 405 nm ($A_{405}$) using the ELISA reader (Titertek Multiscan) after 45 min of incubation with the substrate p-nitrophenyl. Inclusion bodies of BYMV were stained by immersing epidermal strips from the undersides of leaves of *V. faba* cv. Ukko in a solution containing 0.5% Trypan blue and 0.9% NaCl.

### Statistical analysis

Analysis of variance was used for statistical analysis, and calculations of the least significant differences (LSD) of the $A_{405}$ values were made where appropriate (STEEL and TORRIE 1981).

## Results

The isolates BYMV-G, BYMV-Vf and BYMV-Ps were distinguished by the symptoms they caused in test plants (Table 1). In all the pea cultivars tested, BYMV-Ps caused bright yellow mosaic symptoms, whereas BYMV-Vf caused mainly green mosaic and sometimes mild yellow mosaic symptoms (Fig. 2). However, BYMV-G caused only very mild mosaic symptoms and vein clearing. Similarly, BYMV-Vf and BYMV-Ps caused severe green mosaic symptoms in the broad bean cv. Ukko, and the symptoms of BYMV-Vf were visible sooner than those of BYMV-Ps. In contrast, broad bean plants infected with BYMV-G became slightly pale and showed no other symptoms. BYMV-Vf and BYMV-Ps infected *Trifolium pratense* cv. Bjursele

Table 1. Symptoms in test plants caused by isolates of BYMV from *Gladiolus* (G), *Vicia faba* (Vf) and *Pisum sativum* (Ps).

| | BYMV-G | BYMV-Vf | BYMV-Ps |
|---|---|---|---|
| *Phaseolus vulgaris* cv. Dufrix | LRSr, LVN, SM, St | SRSg, SM, St | SRSg, SM, St |
| *Nicotiana benthamiana* | MM / SSI | SM | SM |
| *Pisum sativum* | MM, VCl | GM | YM |
| *Vicia faba* cv. Ukko | SSI | GM | GM |
| *Chenopodium amaranticolor* | LL | - | LL |

LL = local lesions
LRSr = local ring spots with red margins
LVN = local vein necrosis
GM = green mosaic
SM = systemic mosaic
YM = yellow mosaic
SRSg = systemic ring spots with green margins
SSI = systemic symptomless infection detected by ELISA
St = stunting
VCl = vein clearing

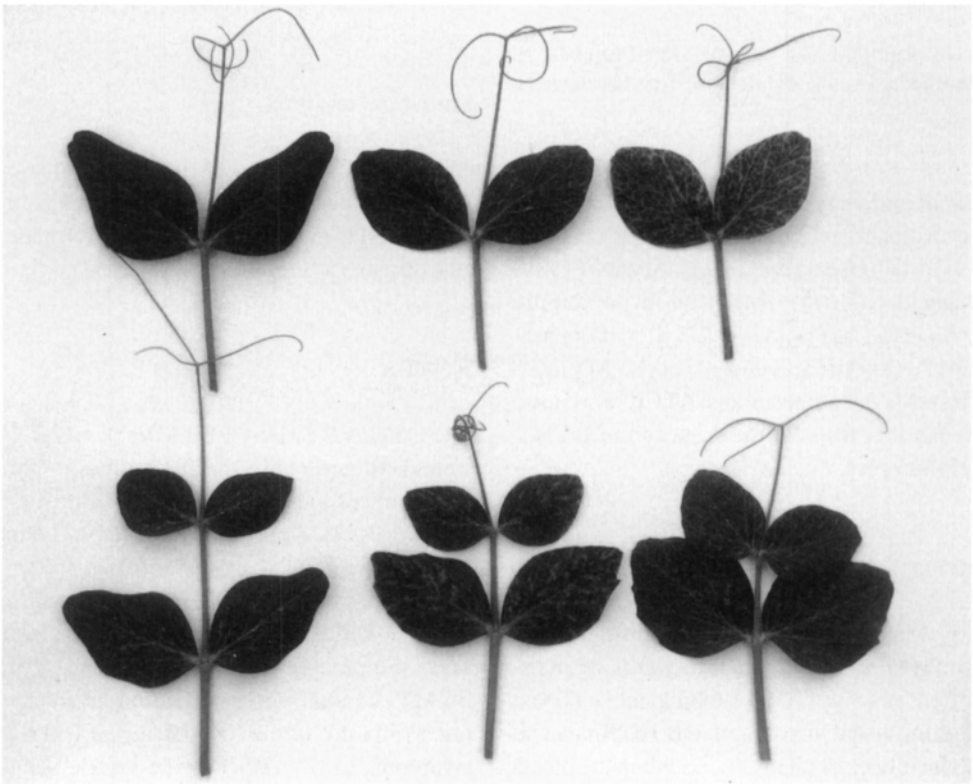

Fig. 2. Leaves of the pea cvs. Proco (upper row) and Hemmo (lower row) systemically infected with BYMV-Ps (right) showing yellow mosaic symptoms, and with BYMV-Vf (middle) showing green mosaic symptoms following sap-inoculation (on the left: leaves from non-inoculated plants).

Table 2. Mean absorbance values from ELISA for detection of BYMV in plants each of eight pea cultivars grown in a screenhouse (a) and glasshouse (b) and also in *P. vulgaris* cv. Dufrix grown in a glasshouse (b) 18 days post-inoculation. The BYMV isolates were from *Gladiolus* (G), *Vicia faba* (Vf) and *Pisum sativum* (Ps). The least significant differences are given at the risk level of 1% ($LSD_{0.01}$).

| | BYMV-G | | BYMV-Vf | | BYMV-Ps | |
|---|---|---|---|---|---|---|
| | Exp. A | Exp. B | Exp. A | Exp. B | Exp. A | Exp. B |
| **(a)** | | | | | | |
| Helka | 0.09 | 0.16 | 0.37 | 0.33 | 0.61 | 0.40 |
| Hemmo | 0.10 | 0.13 | 0.63 | 0.18 | 0.71 | 0.45 |
| Hovi | 0.08 | 0.13 | 1.96 | 0.98 | 0.63 | 0.43 |
| Kalle | 0.16 | 0.16 | 2.00 | 1.27 | 0.85 | 0.74 |
| Pika | 0.12 | 0.16 | 1.14 | 0.28 | 0.23 | 0.67 |
| Proco | 0.15 | 0.11 | 0.37 | 0.29 | 0.14 | 0.59 |
| Solara | 0.08 | 0.17 | 0.94 | 0.31 | 0.68 | 0.40 |
| Tammi | 0.12 | 0.20 | 0.46 | 0.18 | 0.51 | 0.28 |
| uninoculated controls | 0.02 | 0.00 | 0.02 | 0.00 | 0.02 | 0.00 |
| $LSD_{0.01}$ = 0.33 for Exp. A and 0.08 for Exp. B | | | | | | |
| **(b)** | | | | | | |
| Helka | 0.62 | 0.36 | 0.57 | 0.35 | 0.52 | 0.48 |
| Hemmo | 0.67 | 0.42 | 0.28 | 0.20 | 0.26 | 0.28 |
| Hovi | 0.70 | 0.35 | 0.25 | 0.39 | 0.36 | 0.36 |
| Kalle | 1.41 | 0.44 | 0.32 | 0.65 | 0.46 | 0.26 |
| Pika | 0.72 | 0.38 | 0.25 | 0.21 | 0.22 | 0.39 |
| Proco | 0.71 | 0.31 | 1.91 | 1.62 | 0.28 | 0.40 |
| Solara | 0.64 | 0.40 | 0.52 | 0.33 | 0.38 | 0.72 |
| Tammi | 0.69 | 0.52 | 0.18 | 0.24 | 0.31 | 0.51 |
| uninoculated controls | 0.01 | 0.00 | 0.01 | 0.00 | 0.01 | 0.00 |
| *P. vulgaris* cv. Dufrix | | | | | | |
| sap dil. 2 x $10^{-1}$ | 0.65 | 0.48 | 1.10 | 1.17 | 1.25 | 1.71 |
| 2 x $10^{-2}$ | 0.58 | 0.19 | 0.75 | 0.79 | 0.65 | 0.83 |
| 2 x $10^{-3}$ | 0.36 | 0.03 | 0.50 | 0.33 | 0.14 | 0.39 |
| 2 x $10^{-4}$ | 0.18 | 0.00 | 0.06 | 0.09 | 0.04 | 0.09 |
| $LSD_{0.01}$ = 0.17 for Exp. A and 0.42 for Exp. B | | | | | | |

causing systemic vein chlorosis and yellowing, but no infection with BYMV-G was detected. The leaves of *P. vulgaris* L. cv. Dufrix inoculated with BYMV-G produced local ringspots and vein necrosis, but those inoculated with BYMV-Vf or BYMV-Ps remained symptomless. All the BYMV isolates infected *Lupinus luteus* L. causing systemic green mosaic symptoms, narrowing of leaflets and severe stunting. In *Nicotiana tabacum* L. cv. Samsun, all the BYMV isolates caused local symptomless infection which was detected by ELISA, but no systemic infection.

The mean lengths of 50 particles of the BYMV-G, BYMV-Vf and BYMVPs isolates were 781 nm, 778 nm and 816 nm, respectively, in sap prepared for ISEM from systemically infected leaves of *P. vulgaris* cv. Dufrix. Morphologically identical intranuclear inclusion bodies were detected in the epidermic cells of BYMV-infected *V. faba* cv. Ukko with all the BYMV isolates (Fig. 3).

The $A_{405}$ values for the detection of BYMV-Vf and BYMV-Ps differed significantly between many pea cultivars (Table 2). However, symptoms among the cultivars infected with BYMV-Vf or BYMVPs were similar. Thus, the virus titres did not correlate with the severity of symptoms. The concentration of BYMV-G was clearly increased, whereas the concentration of BYMV-Ps was slightly depressed, in pea plants grown in the higher glasshouse temperatures compared to plants grown in the cool screenhouse. In most of the plant species tested, the A405 values from ELISA for the detection of

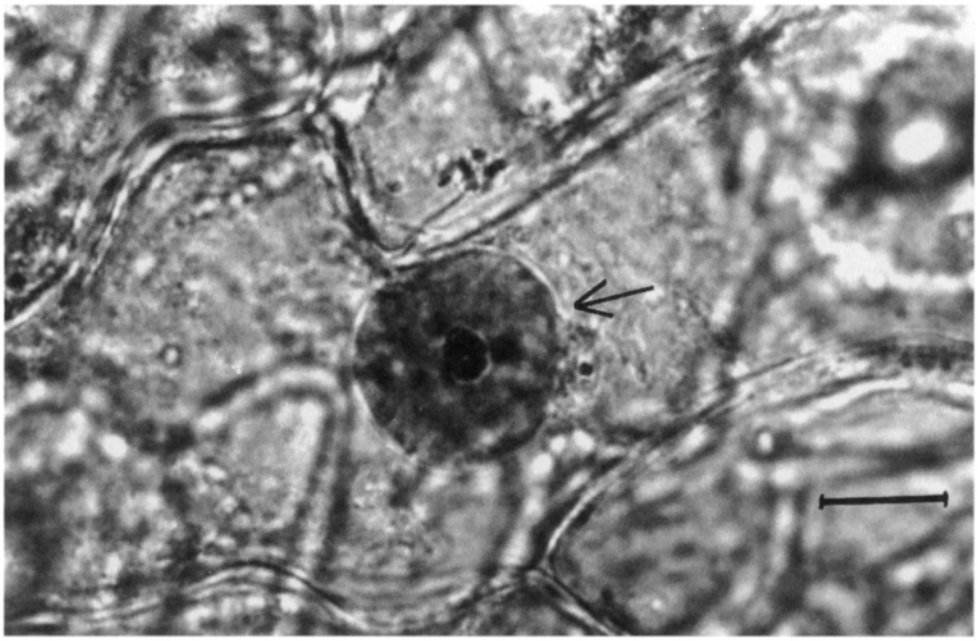

Fig. 3. An intensely stained enlargened nucleolus containing granular inclusion bodies in a weaker stained nucleus (arrow) in an epidermic cell of *V. faba* cv. Ukko systemically infected with BYMV-Vf (bar = 10 µm).

BYMV-G were lower than those for the other two BYMV isolates. However, sap-inoculation of BYMV-G and BYMV-Ps from *L. luteus,* pea cv. Kalle and *P. vulgaris* cv. Dufrix to *C. amaranticolor* Coste et Reyn resulted in similar numbers of local lesions, indicating that the titres of infective virus were similar.

## Discussion

The isolates BYMV-G, BYMV-Vf and BYMV-Ps were clearly distinguished from each other by the symptoms they caused in various test plant species. The symptoms in pea plants and the slightly longer particles of the BYMV-Ps isolate were similar to those of the pea mosaic strains of BYMV previously described, and the symptoms caused by BYMV-Vf in the test plants resembled those described for the bean strain of BYMV (BOS 1970a,b, TAPIO 1970). As with other potyviruses, the length of BYMV particles in plant extracts is affected by the concentration of magnesium ions in the extraction buffer (GOVIER and WOODS 1971). On the other hand, BYMV-G differed from the other two BYMV isolates by its milder symptoms in most of the test plant species, and also serologically, as has been reported previously for other BYMV isolates (JONES and DIACHUN 1977). However, all the isolates reacted with the antibodies raised against BYMV (obtained from M. Albrechtsen and ATCC), but not with those raised against bean common mosaic virus (obtained from L. Bos and D.Z. Maat, Institute for Phytopathological Research (IPO), Wageningen, The Netherlands; data not shown). The intranuclear inclusion bodies produced by all the virus isolates were identical and similar to those previously described for BYMV (BOS 1969, CHANG et al. 1988). Therefore, all the virus isolates represented distinct strains of a single virus species, namely BYMV.

All the recently released pea cultivars of APBF included in the present study were susceptible to BYMV, suggesting that little or no improvement in resistance to BYMV has occured during the last decades and since the previous studies by TAPIO (1970). However, yield losses caused by BYMV in pea are potentially high in Finland, and the virus is

readily spread by aphids from forage legumes to peas in the field, red clover acting as the main virus reservoir (TAPIO 1970). Globally, BYMV is considered one of the most important pathogens of pea, particularly in older cultivars lacking resistance to BYMV (HAMPTON 1984). Aphicides are ineffective in decreasing the spread of the nonpersistently transmitted viruses such as BYMV, but treatment of plants with mineral oil may be more successful (COCKBAIN 1983, JAYASENA and RANDLES 1985). However, resistance to BYMV in pea remains to be developed for virus control in the field. Indeed, since 1965 the recessive gene pair mo/mo conferring resistance to BYMV in *P. sativum* has been routinely incorporated into new pea cultivars in many pea breeding programmes abroad, which is the primary reason to consider BYMV as a minor pathogen of pea at the present (MARX and PROVVIDENTI 1979, HAMPTON 1984). As the domestic cultivation of pea is limited in Finland (7700 ha in 1990, HOVINEN 1990), breeding of peas in Finland should meet the requirements of an international market area to strengthen the economic basis of the breeding programme. Lack of resistance to viruses may be one of the obstacles reducing the adaptability of Finnish pea varieties for cultivation abroad. Genetically engineered virus resistance, such as coat protein mediated resistance to BYMV, is also becoming available in peas in the future (HAMMOND and KAMO 1991, CECCHINI et al. 1992, HULL and DAVIES 1992).

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Jari Valkonen
Department of Plant Production
P.O. Box 27, Viikki
FIN-00014 University of Helsinki, Finland

SELOSTUS

# Kolmen pavun keltamosaiikkivirusrodun oireet ja pitoisuus kahdeksassa hernelajikkeessa

JARI VALKONEN

Helsingin yliopisto

Anttilan kasvinjalostuskoetilan (aiemmin Hankkijan kasvinjalostuslaitos) koekentiltä kerätyistä hernenäytteistä eristettiin pavunkeltamosaiikkiviruksen herneenmosaiikkirotu (BYMV-Ps) ja härkäpapunäytteistä papurotu (BYMV-Vf). Virusten ja virusrotujen määritys perustui testikasvien oireisiin, elektronimikroskopialla havaittuun virushiukkasten kokoon ja muotoon, virusten härkäpavun epidermissolukon tumissa muodostamien inkluusiokappaleiden morfologiaan ja virusten reagointiin vasta-aineiden kanssa serologisissa testeissä. Tanskasta saatu Gladioluksesta eristetty BYMV-isolaatti (BYMV-G) osoittautui testeissä omaksi rodukseen.

BYMV-roduilla inokuloitiin kahdeksan hernelajiketta, joista Helka, Hovi, Pika ja Tammi olivat Hankkijan 1980-luvulla kauppaan laskemia afila-tyyppisiä (puolilehdettömiä) lajikkeita, Kalle 1950-luvulla ja Hemmo 1980-luvulla kauppaan tulleita perinteisen lehtityypin omaavia lajikkeita, sekä Solara afila-tyyppinen ja Proco perinteisen lehtityypin omaava Suomessa yleisesti viljeltävä hollantilainen hernelajikke. Kaikki BYMV-rodut infektoivat kaikki testatut hernelajikkeet. BYMV-Ps aiheutti herneissä voimakkaat keltakirjo-oireet ja BYMV-Vf viherkirjo-oireita, mutta BYMV-G aiheutti vain lievää viherkirjoa tai selkeäsuonisuutta. Saman virusrodun pitoisuus vaihteli lajikkeesta toiseen, mutta viruspitoisuus ja oireiden voimakkuus eivät korreloineet.

Tutkimus osoitti, että suomalaisten hernelajikkeiden BYMV-kestävyys ei ole kehittynyt 1960-luvulla tehtyjen tutkimusten jälkeen. BYMV ja erityisesti sen herneenmosaiikkirodut aiheuttavat merkittäviä satotappioita hernelajikkeissa, jotka ovat virukselle alttiita. Sen vuoksi useissa ulkomaisissa herneenjalostusohjelmissa BYMV-kestävyyden tuottavien geenien siirtoa uusiin jalosteisiin on tehty rutiininomaisesti 1960-luvulta asti. Virustautikestävyyden lisääminen parantaisi todennäköisesti suomalaisten hernejalosteiden kilpailukykyä ulkomaisilla markkinoilla.