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The response of plant species used in agriculture and horticulture to viroid infections

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Abstract

The reactions of the viroids causing cucumber pale fruit (CPFV), chrysanthemum stunt (CSV) and citrus exocortis (CEV) in different plant species and varieties used in agriculture and horticulture were studied. These viroids caused identical symptoms on tomato and potato. The reactions of chrysanthemum 'Mistletoe' to CPFV or CSV were identical, but CEV-infected plants reacted quite differently. CPFV and CEV caused the same type of symptoms on cucumber plants but symptoms of CEV were always weaker.

Ten of the tested horticultural crop species appeared to be susceptible to CPFV, of which eight produced symptoms. In the Netherlands, however, CPFV is only described as pathogen on cucumber plants grown in glasshouses. Ten species were susceptible to CSV of which three produced symptoms. In the Netherlands CSV only occurs in chrysanthemum. Nine of the tested crops proved to be susceptible to CEV and seven were sensitive to this viroid which occurs in citric crops of (sub)tropical climate zones.

Our results show that the viroids studies form potential pathogens for other crops than cucumber and chrysanthemum which are now affected by two of them.

Additional keywords: chrysanthemum stunt viroid, citrus exocortis viroid, cucumber pale fruit viroid.

Introduction

In the last decade, several investigations were made on the pathogens eliciting potato spindle tuber (Diener, 1971), citrus exocortis (Sänger, 1972; Semancik and Weathers, 1972), chrysanthemum chlorotic mottle (Romaine and Horst, 1975), hop stunt (Sasaki and Shikata, 1977), cucumber pale fruit (Van Dorst and Peters, 1974) and chrysanthemum stunt (Diener and Lawson, 1973; Hollings and Stone, 1973). These diseases are all caused by viroids.

Viroids consist of closed single-stranded circular RNA molecules with a molecular weight of about 120000 (Sänger et al., 1976). Recently, the nucleotide sequence of an isolate of potato spindle tuber viroid (PSTV) has been established (Gross et al., 1978). Little attention has been paid to the biological behaviour of viroids. There is hardly any information available concerning the relationships between the different viroid isolates. Only two comparative studies (Singh and Clark, 1973; Dickson et al. 1975) have been published concerning PSTV and citrus exocortis viroid (CEV).

The occurrence of pale fruit disease in cucumber and stunt in chrysanthemum in the Netherlands prompted a study on how other crops might react following infection with

these viroids. CEV was included in the investigation for comparative purposes and to broaden the scope of the study. This paper is concerned with the pathogenicity of CEV, cucumber pale fruit viroid (CPFV), and chrysanthemum stunt viroid (CSV) particularly on horticultural crops.

Materials and methods

The isolate of CEV originally supplied by H. L. Sänger (Justus Liebig University, Giessen, Fed. Rep. of Germany), was maintained in *Gynura aurantiaca*. CPFV isolated by Van Dorst and Peters (1974) from cucumber was maintained in the same host. CSV was obtained from F. A. Hakkaart (Research Station for Floriculture, Aalsmeer), and kept in *Chrysanthemum morifolium* 'Mistletoe'.

Test plants were grown for 3 months in 0.75 l pots containing a peat/sand growth mixture. Plants were supplied with fertilizer weekly. The fertilizer was a mixture of N, P_2O_5, K_2O and MgO, in the ratio of 15:5:15:6 parts in water. All plants were raised in a greenhouse at 25–35 °C at a relative humidity of 40–80% with supplementary lighting provided in the winter months. A range of species from several families was investigated in this study. The species tested were from the Caryophyllaceae, Chenopodiaceae, Compositae, Cruciferae, Cucurbitaceae, Gramineae, Iridaceae, Liliaceae, Papilionaceae, Rosaceae, Solanaceae, Umbelliferae and Vitaceae.

Ten plants from each species were selected for inoculation with each of the viroids when they were 10–20 cm high. Inoculations were made by the slashing method using sterile razorblades (Semancik and Weathers, 1972). Fifteen slashes were made from diseased plants to the stems of healthy plants. Backinoculations from these plants were made three to four weeks later; CEV, CPFV and CSV being assayed on *G. aurantiaca*, *Cucumis sativus* 'Sporu' and *C. morifolium* 'Mistletoe' respectively. Following these inoculations cucumber plants were kept for 1 month, *Gynura* plants for 2 months, and chrysanthemum for 3 months to allow for the development of symptoms.

Results

The susceptibility and/or sensitivity of several Solanaceous species is given in Table 1. Most of the species tested were susceptible to CPFV, CSV or CEV. All three viroids produced stunting on tomato plants. The stunting on 'Moneydor' was less severe than on 'Rutgers'. The symptoms in tomato 'Rutgers' were similar to those reported for CEV (Singh and Clark, 1973) and PSTV infections (Raymer and O'Brien, 1962). CPFV, CSV and CEV caused identical symptoms on potato 'Arka' with a severe stunting and chlorosis in the youngest leaves of the plants (Fig. 1).

Potato tubers 'Katahdin' infected with either of the viroids were planted in successive years and observed annually. Foliage and tubers showed no symptoms in the first three years but in the fourth year healthy plants produced more foliage than those grown from infected tubers.

The eggplant variety 'Mammouth' displayed symptoms after infection with CPFV as shown in Fig. 2, when grown at 20–25 °C. In the oldest leaf on which symptoms appeared, necrosis occurred in the smaller veins, which was followed by an interveinal chlorosis. The younger leaves were malformed but the midribs remained unimpaired. Lower temperatures resulted in a longer incubation period and weaker symptoms.

Fig. 1. A potato plant of the variety Arka showing severe stunting and rosette in the top after infection with cucumber pale fruit viroid (CPFV).

Fig. 2. Severe necrosis and degeneration of leaf tissue caused by cucumber pale fruit (CPFV) in the eggplant variety Mammouth.

Fig. 1. Dwerggroei en rosetvorming in de bovenste delen van een aardappelplant van het ras Arka na infectie met het bleke-vruchtviroïde van komkommer (CPFV).

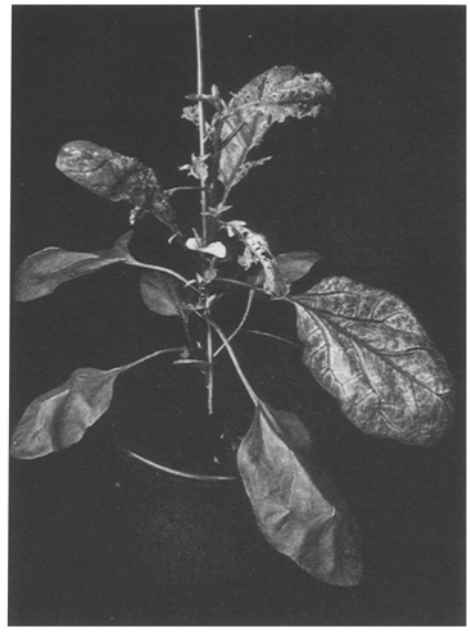

Fig. 2. Hevige degeneratie en necrose van bladmoes en -nerven van een aubergineplant van het ras Mammouth na infectie met het bleke-vruchtviroïde van komkommer.

Although CPFV was present in the eggplants, no symptoms appeared when the temperature rose above 25°C. The eggplant variety 'Mammouth' was also susceptible to CEV, but not to CSV.

Thirteen other eggplant varieties were tested viz.: Yersey King, Caminal, Short Tom, Paarse Dwerg, Bulgaarse, Early Prolific, Nagaoka, Kimo, Balvreine, Lange Violette, Vedette, Claresse and Poeldijks Glorie. All but 'Poeldijks Glorie' proved to be susceptible to CPFV, 'Short Tom', 'Bulgaarse' and 'Kimo' were susceptible to CEV and 'Yersey King' was susceptible to CSV. *Solanum ovigerum* was only susceptible to CEV.

The viroids could not be recovered from *Solanum dulcamara* 'Rupestre'. Sweet pepper and petunia produced no symptoms after inoculation with CPFV, CSV or CEV, but backtests indicated that the viroids could be recovered from the inoculated plants. Eight other petunia species were also susceptible to CPFV: *Petunia violaceae* 'Cacadu', *P. inflata, P. parviflora, P. nyctaginiflora, P. hybrida* (Hook) Vilm, *P. hybrida* Hort., *P. atkinsiana* and *P. axillaris*. *Petunia inflata, P. nyctaginiflora, P. hybrida* Hort. and *P. axillaris* were susceptible to CSV. Susceptibility of petunia to CEV was not tested. *Nicandra physaloides* was susceptible to CSV and CEV.

Table 1. Susceptibility and sensitivity of some Solanaceous species to three viroids.

Species tested	CPFV		CSV		CEV	
	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant
Tomato (*Lycopersicon esculentum* Mill 'Rutgers')	+	5/5	+	5/5	+	2/5
Tomato (*Lycopersicon esculentum* Mill 'Moneydor')	+	4/5	+	1/5	+	2/5
Potato (*Solanum tuberosum* 'Arka')	+	2/2	+	2/2	+	2/2
Potato (*Solanum tuberosum* 'Katahdin')	–	6/6	–	4/5	–	5/5
Eggplant (*Solanum melongena* 'Mammouth')	+	7/10	–	0/4	–	4/4
Eggplant (*Solanum ovigerum*)	–	0/10	–	0/10	–	8/10
Bittersweet (*Solanum dulcamara* 'Rupestre')	–	0/6	–	0/6	–	0/10
Sweet pepper (*Capsicum annuum* 'Verbeterde Glas')	–	14/50	–	3/20	–	1/5
Petunia (*Petunia hybrida*)	–	9/10	–	1/10	–	0/10
Apple-of-Peru (*Nicandra physaloides*)	–	0/5	–	3/5	–	1/4

Tabel 1. Vatbaarheid en gevoeligheid van een aantal Nachtschade-achtigen voor drie viroïden.

Table 2. Susceptibility and sensitivity of some Compositae species to three viroids.

Species tested	CPFV		CSV		CEV	
	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from textplant
Chrysanthemum (*Chrysanthemum morifolium* 'Mistletoe')	+	3/5	+	6/6	+	1/5
Chrysanthemum (*Chrysanthemum morifolium* 'Spider')	–	0/20	–	0/20	+	7/20
Gynura aurantiaca	–	2/5	–	1/5	+	5/5
Lettuce (*Lactuca sativa* 'Deci-Minor')	–	0/8	–	0/10	–	0/14
Chicory (*Cichorium intybus*)	–	0/10	–	0/10	–	0/10
Endive (*Cichorium endivia* 'Volhart')	–	0/10	–	0/10	–	0/10

Tabel 2. Vatbaarheid en gevoeligheid van een aantal Samengesteldbloemigen voor drie viroïden.

Fig. 3. Mottling and leaf deformation in the top leaves of plants of the chrysanthemum variety Mistletoe infected with citrus exocrotis viroid (CEV).

Fig. 3. Bladdeformatie en vlekkerigheid van de topbladeren na infectie van de chrysant Mistletoe met het viroïde dat citrus exocortis veroorzaakt.

Some species from the Compositae were also tested for their susceptibility and sensitivity to viroids (Table 2). Several Compositae tested proved to be susceptible to one or more of the viroids used. The symptoms in chrysanthemum 'Mistletoe' caused by CPFV or CSV were identical to those described for CSV by Hollings and Stone (1973). However, completely different symptoms were produced by CEV. The plants showed severe growth reduction and leaf deformation in the top leaves which were flecked by yellow spots and crinkled (Fig. 3). These spots were smaller and less clear than the spots caused by CSV or CPFV. Chrysanthemum 'Spider' became heavily stunted after infection with CEV.

No symptoms were observed when *G. aurantiaca* was infected by CPFV or CSV but the viroids could be recovered, indicating that this species is also susceptible to other viroids apart from CEV. The symptoms caused by CEV on *G. aurantiaca* were identical to those described by Semancik and Weathers (1972).

Lettuce and chicory did not produce symptoms after infection with CPFV, CSV or CEV, neither could the viroids be recovered from the inoculated plants. Endive appeared to be susceptible to CSV only.

The results obtained after the inoculations of some Cucurbitaceous species are shown in Table 3. Out of the eight species tested seven proved to be sensitive to CPFV and one was susceptible. CEV caused symptoms on two species whereas the other six species tested were only susceptible to CEV. Only three species appeared to be susceptible to CSV.

The symptoms caused by CPFV on cucumber were the same as those described by Van Dorst and Peters (1974) and CEV caused a similar reaction on cucumber although the symptoms were much weaker. The symptoms caused by CPFV on gherkin, melon and two *Benincasa* species have previously been described by Van Dorst and Peters (1974) and were identical in this study.

Table 3. Susceptibility and sensitivity of some Cucurbitacous species to three viroids.

Species tested	CPFV		CSV		CEV	
	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant
Cucumber (*Cucumis sativus* 'Sporu')	+	10/10	–	5/10	+	2/3
Cucumber (*Cucumis sativus* 'Tablegreen')	+	8/8	–	0/5	–	6/10
Gherkin (*Cucumis sativus* 'Kora')	+	9/10	–	0/10	–	2/10
Gherkin (*Cucumis sativus* 'Baarlose Nietplekker')	+	9/10	–	1/10	+	8/10
Melon (*Cucumis melo* 'Ogen')	–	9/10	–	0/10	–	1/10
Melon (*Cucumis melo* 'Suiker')	+	10/10	–	0/10	–	10/10
Benincasa cerifera	+	5/5	–	2/5	–	1/5
Benincasa hispida	+	6/7	–	0/7	–	4/9

Table 3. Vatbaarheid en gevoeligheid van een aantal Komkommerachtigen voor drie viroïden.

Table 4. Susceptibility and sensitivity of broad bean, pea, parsley and celery to CEV.

Species tested	CEV	
	symptomproduction on testplant	recovery from testplant
Broad bean (*Vicia faba* 'Mezala')	–	5/5
Pea (*Pisum sativum* 'Wonder van Amerika')	–	6/6
Parsley (*Petroselinum sativum*)	–	3/10
Celery (*Apium graveolens*)	+	2/10

Tabel 4. Vatbaarheid en gevoeligheid van tuinboon, erwt, peterselie en selderij voor citrus exocortis viroid.

Gherkin 'Baarlose Nietplekker' which was infected with CEV reacted by producing distorted flowers without any symptom on the leaves.

No differences in symptoms were noticed on the Cucurbitaceous plants infected with CPFV or CEV, but the symptoms produced by CPFV were always more severe.

The reactions of the broad bean variety 'Mezala', pea variety 'Wonder van Amerika' and parsley following infection with CEV are recorded in Table 4. These species were susceptible to CEV. Celery produced symptoms after infection with CEV, which consisted of severe growth reduction, yellowing of the leaves and hyper-sprouting (Fig.

Fig. 4. A celery plant (left) infected with citrus exocortis viroid (CEV) and a healthy plant (right).

Fig. 4. Een gezonde selderijplant (rechts) en één besmet met het viroïde dat citrus exocortis veroorzaakt.

4). CPFV and CSV were not able to infect these species since no infectious material could be recovered from inoculated plants.

The following species were tested and appeared not to be susceptible to CPFV, CSV or CEV, French bean (*Phaseolus vulgaris*), scarlet bean (*Phaseolus coccineus*), cauliflower (*Brassica oleracea* var. *botrytis*), Brussels sprouts (*Brassica oleracea* var. *gemmifera*), kohlrabi (*Brassica oleracea* var. *gongylodes*), radish (*Raphanus sativus*), carrot (*Daucus carota*), self-blanching celery (*Apium graveolens* var. *dulce*), leek (*Allium porrum*), beetroot (*Beta vulgaris* var. *rubra*), pear (*Pyrus communis*), apple (*Pyrus malus*), grape (*Vitis vinifera*), rose (*Rosa* species), freesia (*Freesia refracta*), lily (*Lilium* species), tulip (*Tulipa* species), hyacinth (*Hyacinthus orientalis*), Chinese carnation (*Dianthus chinensis*), carnation (*Dianthus caryophyllus*), wheat (*Triticum aestivum*), oat (*Avena sativa*), barley (*Hordeum vulgare*) and rye (*Secale cereale*).

Discussion

Out of the 53 arbitrarily chosen species tested, 18 proved to be susceptible to CPFV and 12 were sensitive to this viroid, 13 and 4 were susceptible and sensitive for CSV, while 25 and 9 for CEV, respectively. The observations on susceptibility and sensitivity of some species and varieties tested, are summarized in Table 5.

It should be noted that the results of this investigation might have been different if the viroids had been obtained from other hostplants. Indeed, a host adaptation of CPFV was noticed when the viroid was serially passaged through various hosts. Symptom production on plants was affected following serial passage of CPFV (Peters and Runia, in preparation). To avoid these passage-effects tomato plants were used as source for the viroids when tomato and potato 'Arka' plants were inoculated.

The results with CSV may also have been influenced in a negative way by the use of chrysanthemum as test plant. Grafting to viroid-free 'Mistletoe' chrysanthemum is the most reliable method of detecting CSV (Hollings and Stone, 1973). Since most species tested in this study could not be grafted to chrysanthemum, infected plants of some species may have escaped detection.

It can be concluded from this investigation that the viroids CEV, CPFV and CSV differ in ability to infect the different hosts tested. The symptoms produced on the species and varieties sensitive to these viroids were alike except for those on chrysanthemum 'Mistletoe'. CEV produced on 'Mistletoe' a symptom that differed from those caused by CSV and CPFV.

The differences observed between susceptibility and sensitivity of the various plant species suggest that the three viroids are different. Differences may be small, however, since the symptoms produced on potato and tomato by these viroids indicate a close similarity of biological activity at least in these hosts.

In comparative studies of PSTV and CEV, Singh and Clark (1973) observed that both agents produced identical symptoms in *Scopolia* species, petunia, potato and tomato. The authors also noticed that symptoms in *G. aurantiaca* were identical although they appeared in PSTV infected plants some two weeks later when compared to CEV infected plants. Some *Gynura* plants, however, inoculated with PSTV developed only slight stunting and not the pronounced symptoms characteristic of CEV-infected plants. Singh and Clark thus concluded that PSTV and CEV were closely related strains of a single pathogenic agent. However, an analysis of PSTV and CEV by

Table 5. Differences in susceptibility and sensitivity of a number of plant species and varieties used in horticulture to three viroids.

Species tested	CPFV		CSV		CEV	
	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant	symptom-production on test-plant	recovery from testplant
Cucurbitaceae						
Cucumber 'Sporu'	+	+	−	+	+	+
Cucumber 'Tablegreen'	+	+	−	−	−	+
Gherkin 'Baarlose Nietplekker'	+	+	−	+	+	+
Gherkin 'Kora'	+	+	−	−	−	+
Benincasa hispida	+	+	−	−	−	+
Benincasa cerifera	+	+	−	+	−	+
Melon 'Suiker'	+	+	−	−	−	+
Melon 'Ogen'	−	+	−	−	−	+
Solanaceae						
Eggplant 'Mammouth'	+	+	−	−	−	+
Eggplant 'Claresse'	−	+	−	−	−	−
Eggplant (*Solanum ovigerum*)	−	−	−	−	−	+
Nicandra physaloides	−	−	−	+	−	+
Compositae						
Chrysanthemum 'Mistletoe'	+	+	+	+	+	+
Chrysanthemum 'Spider'	−	−	−	−	+	+
Gynura aurantiaca	−	+	−	+	+	+
Endive 'Volhart'	−	−	−	+	−	−
Umbelliferae						
Celery	−	−	−	−	+	+
Parsley	−	−	−	−	−	+
Papilionaceae						
Broad bean 'Mezala'	−	−	−	−	−	+
Pea 'Wonder van Amerika'	−	−	−	−	−	+

Tabel 5. Verschillen in vatbaarheid en gevoeligheid van een aantal tuinbouwgewassen voor drie viroïden.

fingerprinting performed by Dickson et al. (1975) showed that the two viroids were not identical. The small differences found in pathogenicity between these viroids may be based on minor differences in their nucleotide sequences or configuaration of RNA.

Thus far there are only two horitcultural crops grown in the Netherlands known to be affected by viroids. CPFV occurs in cucumber and CSV in chrysanthemum. Both crops may form potential viroid reservoirs form which spread to other susceptible crops may occur.

The first CSV-diseased chrysanthemums are always found in mother stock plants which are maintained for propagation. It is unknown how this mother stock primarily becomes infected. Further spread of CSV mainly occurs by mechanical contact from cuttings derived from the infected mother stock (Hollings and Stone, 1973). The number of cucumber plantings affected by CPFV is only a small percentage of the total grown and most diseased plants are found in spring. Initially only a few affected plants are found and then often near the outer walls of glasshouses or close to the main walkways suggesting vector introduction of the viroid. In glasshouses the incubation period is approximately two months. Spread of viroid in glasshouses occurs mechanically through pruning, harvesting and other activities of the grower. Regarding the results presented here it is remarkable that in the Netherlands only chrysanthemums and cucumbers are apparently affected by viroids. More instances of viroid diseases may well be reported in the future.

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Samenvatting

Een vergelijkend onderzoek naar de reactie van cultuurgewassen op de viroïden, die de bleke-vruchtenziekte bij komkommer, chrysante-stunt en citrus-exocortis veroorzaken

Het viroïde dat de bleke-vruchtenziekte bij komkommer veroorzaakt (CPFV), chrysanthemum stunt viroïde (CSV) en citrus exocortis viroïde (CEV) produceren symptomen op tomaat en aardappel, die niet van elkaar zijn te onderscheiden. De reactie van chrysant 'Mistletoe' op CPFV of CSV is identiek, maar na infectie met CEV reageren de planten volkomen anders. Komkommers ontwikkelen dezelfde symptomen na een besmetting met CPFV en CEV, hoewel laatstgenoemd agens altijd een zwakker ziektebeeld oproept.

Tomaat, aardappel, aubergine, chrysant, komkommer, augurk, meloen en *Benincasa* bleken gevoelig te zijn en paprika en petunia vatbaar voor CPFV, terwijl in Nederland alleen van komkommergewassen bekend is, dat ze aangetast worden door dit pathogeen.

Tomaat, aardappel en chrysant waren ook gevoelig voor CSV, vatbaar voor dit viroïde waren paprika, petunia, *Nicandra*, andijvie, komkommer, augurk en *Benincasa cerifera*. In ons land kennen we stunt alleen in de chrysantenteelt. Negen gewassen bleken vatbaar te zijn voor CEV, en zeven waren gevoelig voor dit viroïde, dat alleen in (sub)tropische klimaatzones voorkomt.

Vierentwintig cultuurgewassen bleken onvatbaar te zijn voor alle drie viroïden. De resultaten van dit onderzoek wijzen er op dat CPFV, CSV en CEV nauw verwant zijn, maar niet identiek.

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