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Yellows of lettuce and some other vegetable crops in the Netherlands caused by beet western yellows virus

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Abstract

A virus isolated from lettuce (*Lactuca sativa*), endive (*Cichorium endivia*), witloof chicory (*C. intybus*), and spinach (*Spinacia oleracea*), and from some weeds was shown to be beet western yellows virus (BWYV) by its host range, particle morphology and serology. It resembled previously described European isolates but differed from American strains in its inability to infect *Beta vulgaris, Brassica pekinensis* and *Raphanus sativus*. The most useful host for routine indexing was *Crambe abyssinica*. Virus particles in purified preparations stained with uranyl acetate were isometric, ca. 27 nm in diameter. Purified virus reacted with antiserum to an American strain of BWYV in infectivity neutralization, gel diffusion and serologically specific electron-microscopy tests.

The field reaction to BWYV of cultivars of lettuce, other *Lactuca* species and some *Cichorium* species was investigated and differences in symptom expression were observed. On the basis of observations during two seasons BWYV appeared to be widely distributed but seemed of minor economic importance to lettuce growing. It may be a potentially important pathogen of endive and chicory.

Additional keywords: Cichorium endivia, C. intybus, Crambe abyssinica.

Introduction

Premature yellowing of some plants in lettuce crops (*Lactuca sativa*) in the Netherlands has been noticed for many years (Bos and Ashby, 1978) and has often been attributed to iron or magnesium deficiency. Symptoms usually occur late during crop development. Outer leaves of affected plants are then strikingly chlorotic with a markedly green venation (Fig. 1). Depending on time of infection, plants may be reduced in size and become worthless. Leaf chlorosis especially attracts attention in left-over bolting plants or in plants grown for seed (Fig. 2). Similar symptoms are sometimes observed in individual plants of endive crops (*Cichorium endivia*). Here stunting may be very pronounced. During 1978 our attention was drawn to comparable symptoms in witloof chicory (*Ci. intybus*). In one crop incidence was ca. 50%. Plants were stunted and chlorotic and interveinal chlorosis in leaves was especially distinct (Fig. 3).

Symptoms in lettuce closely resemble those of 'June yellows' of lettuce in California now known to be due to infection by beet western yellows virus (BWYV) (Duffus, 1960). This virus has subsequently been isolated from lettuce crops with

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Fig. 1. Lettuce plant with beginning symptoms of yellowing after natural infection with BWYV. Left, healthy plant.

Fig. 1. Slaplant met beginnende vergelingssymptomen, na natuurlijke infectie met slavergelingsvirus. Links, gezonde plant.

yellowing symptoms in England (Russell and Duffus, 1970), Germany (Nagi, 1975) and France (Lecoq, 1977). It is aphid-borne in the persistent manner, able to infect over 150 species in 23 dicotyledonous families (Duffus, 1972, 1977), and different isolates vary in reaction on various hosts (Duffus, 1964). BWYV is serologically related to if not identical with turnip yellows virus (Duffus and Russell, 1972) described in Europe by Vanderwalle and Roland (1951) and Heinze (1967).

This paper describes (1) the identification of BWYV from lettuce in the Netherlands by host range, electron microscopy and serology, (2) a comparison of the sensitivity and reliability of various test plants for detection of BWYV, (3) its incidence in lettuce and other hosts, and (4) an assessment of the susceptibility of a number of currently grown lettuce cultivars, other *Lactuca* species and some *Cichorium* species. A brief discussion of BWYV and its relationships to other yellows viruses is also given.

Materials and methods

1. Identity of pathogen

Isolates and transmission. Leaves were collected from three different lettuce samples showing yellowing symptoms and placed in plastic dishes with tight-fitting lids and lined with moistened filter paper. Thirty to fifty non-viruliferous apterae of *M.*

Fig. 2. Striking chlorosis in bolting lettuce plants after natural infection with BWYV. Left, healthy branch.

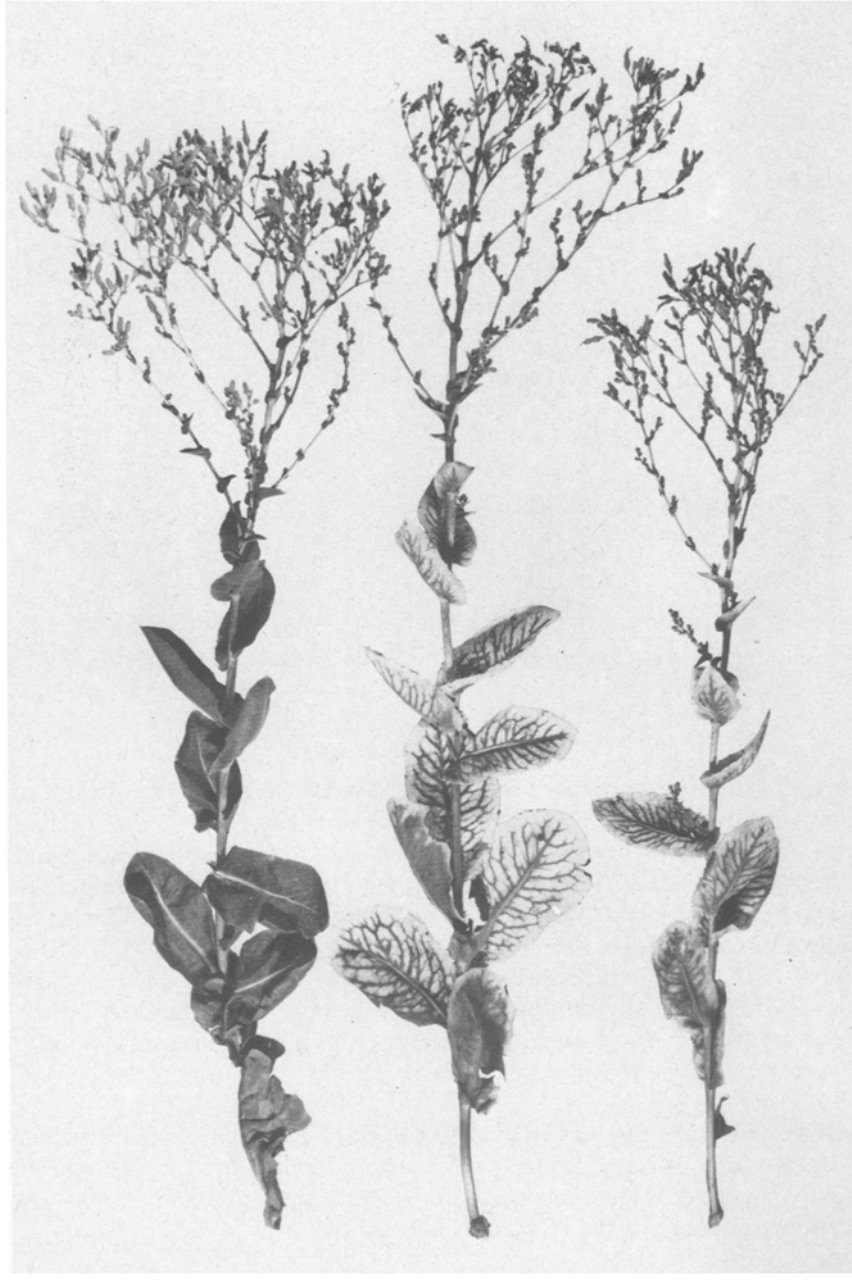

Fig. 2. Opvallende chlorose in doorschietende slaplanten na natuurlijke infectie met slavergelingsvirus. Links, gezonde tak.

Fig. 3. Leaf symptoms in two witloof chicory cultivars after natural infection with BWYV.

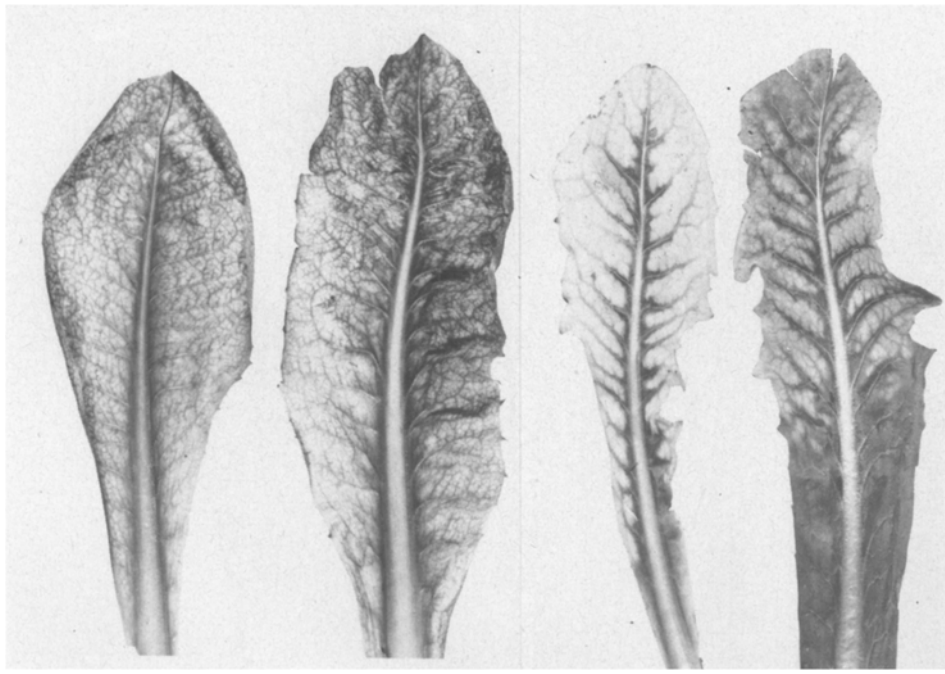

Fig. 3. Bladsymptomen in twee witlofrassen na natuurlijke infectie met slavergelingsvirus.

persicae were allowed to feed on each sample for two days and then transferred to young plants of *Senecio vulgaris*, *Claytonia perfoliata* and *Crambe abyssinica* for two to three days. These three plant species were used as standard indicators throughout this study. Aphids were then killed by spraying with mevinphos or by dipping in nicotine sulphate and the plants were placed in a glasshouse at 20 ± 2°C with 13 h/day of supplementary artificial illumination (20 000 lux: Philips G/92/2 400 w SON/T lamps). The three lettuce isolates of the virus were maintained in these indicators and viruliferous aphids for host range testing were obtained by the procedure outlined above. For isolates from other crops and wild hosts, see under Incidence.

Host range tests. Normally five to ten plants of each plant species listed by other workers as hosts and non-hosts (Table 1) were tested. Plants were sprayed weekly with mevinphos. Symptoms were recorded after four to six weeks and plants were backtested to one or more of the standard indicators.

Purification and electron microscopy. Plants of *Physalis floridana* were inoculated with a lettuce isolate of the virus by aphid transfer and were subsequently propagated by cuttings. Virus was purified from leaf material using the method of Ashby and Huttinga (1979). Drops of purified virus preparations were placed on electron

microscope grids washed with 20 drops of distilled water, and then with 5 drops of 2% unbuffered uranyl acetate. The preparations were examined in a Philips EM 300.

Serology. Purified preparations of the virus were tested against an antiserum (RY-1-R3) to BWYV, supplied by Dr J.Duffus, Salinas, California, using standard Ouchterlony double-diffusion tests in agar gels (1% Oxoid purified agar, 0.85% NaCl, 0.05%NaN_3). Preparations were also examined using the clumping technique of serologically specific electron microscopy as described by Milne and Luisoni (1977).

Leaves of virus-infected *Capsella bursa-pastoris* were dried over calcium chloride and sent to Dr Duffus. These samples were tested by infectivity neutralization (Duffus and Gold, 1965).

2. Comparison of indicator species

The sensitivity and reliability of *Ca. bursa-pastoris, S. vulgaris, Cl. perfoliata* and *Cr. abyssinica* were compared. Five plants of each test species were inoculated using 5, 10, 15, 30 or 50 apterae of *M. persicae* which had previously fed for three days on leaves of *Ci. endivia*, infected with a lettuce isolate of BWYV. Controls consisted of plants infected with 0, 10 and 30 non-viruliferous *M. persicae.* After a 48-h transmission period, all plants were dipped in nicotine sulphate and placed in a glasshouse under conditions stated previously. Symptoms were recorded three and five weeks after inoculation. Plants were regularly dipped in nicotine sulphate or sprayed with mevinphos.

3. Incidence of virus in lettuce crops and other hosts

A preliminary survey of lettuce crops in major lettuce growing areas of the Netherlands was made during summer 1977. An estimate of the percentage of infected plants was made on visual symptoms and representative samples were taken for transmission studies by the procedures already outlined.

In addition, samples were taken from other crops and weeds growing in the vicinity of lettuce. Non-viruliferous apterae of *M. persicae* were fed on suspected host plants and then transferred to *L. sativa* and *Cr. abyssinica.*

A further survey of lettuce crops was undertaken during the 1978 growing season.

4. Reaction of lettuce cultivars

Visual assessment of BWYV-like symptoms on 20 lettuce cultivars was made in mid-September 1977. The trial was at the IPO experimental farm at Lienden and primarily to investigate symptomatology of lettuce mosaic virus (LMV) and cucumber mosaic virus (CMV). Five replicates of 20 plants of each cultivar were planted in mid-May and three similar replicates were planted in mid-June. All plants had been inoculated in the glasshouse with LMV, CMV or with both viruses prior to setting out. In the field considerable natural infection by BWYV occurred. The possible influence of the two other viruses on symptom expression of BWYV has been

ignored since their symptoms were weak and final assessment was intended only to indicate the range of susceptibility to BWYV of the different lettuce cultivars. Susceptibility of selected cultivars was subsequently tested in the glasshouse.

In 1978 a selection of *Lactuca* and *Cichorium* species were tested for resistance to BWYV by (a) planting directly in the field for exposure to natural infection and (b) inoculating in the glasshouse using apterae of *M. persicae* raised on infected *Ca. bursa-pastoris*. The aphids were killed with insecticide after one week and the plants were transferred to the field at Lienden.

Table 1. Host range comparison of various isolates of BWYV and related viruses.

	BMYV from beet (Russel, 1965; Duffus & Russell, 1975)	Turnip YV, English isolate (Duffus & Russell, 1972)	BWYV, USA (Duffus, 1960, 1964)	BWYV, various USA strains (Duffus, 1964)	BWYV from lettuce and weeds, England (Duffus & Russell, 1970)	Netherlands isolates
Chenopodiaceae						
Beta macrocarpa	+	−	+		+ + +	+
Beta vulgaris	+	−	+	+ + + − +	− − −	−
Chenopodium capitatum	−	−	−		− − −	−
Spinacia oleracea	+		+			+
Compositae						
Lactuca sativa	−	+	+	+ + + − +	+ + +	+
Senecio vulgaris	+	+	+	+ + + + +	+ + +	+
Cruciferaceae						
Brassica juncea		+	+		+ + +	+
Brassica pekinensis	−	−	+	− − − + +	− − −	−
Brassica rapa	−	+	+		+ + +	+
Capsella bursa-pastoris	+	+	+	+ + + + +	+ + +	+
Crambe abyssinica	+	+	+		+ +	+
Lepidium lasiocarpum			+			+
Raphanus sativus	−	−	+		− − −	−
Leguminosae						
Trifolium incarnatum	−	+			− + +	+
Portulacaceae						
Claytonia perfoliata	+	+	+		+ + +	+
Solanaceae						
Nicotiana clevelandii	−	+	+		+ + +	+
Physalis floridana		+	+	+ + + + +	+	+
Physalis wrightii			+	+ + + + +		+

Tabel 1. Waardplantvergelijking van verscheidene isolaten van het slavergelingsvirus (BMYV) en verwante virussen.

Results

1. Identity of pathogen

Host range. The reaction of the three Netherlands isolates from lettuce compared with various isolates of BWYV and related viruses is shown in Table 1. The Netherlands isolates had the same host range as isolates reported from lettuce in England and like them differed from most of the American ones in being unable to infect *Beta vulgaris, Brassica pekinensis* and *Raphanus sativus.* The symptoms produced on the various host plants were as described by the other workers listed in Table 1.

Fig. 4. Electron micrographs of partially purified beet western yellows virus stained in 2 % unbuffered uranyl acetate. A) concentrated untreated preparation, B) virus with antiserum to BWYV-USA (diluted: 1 :64) showing dumping of particles, C) virus with antiserum to unrelated cherry leafroll virus (dilution 1 :64) with no apparent clumping; virus concentrations in B and C were identical. Bar represents 100 nm.

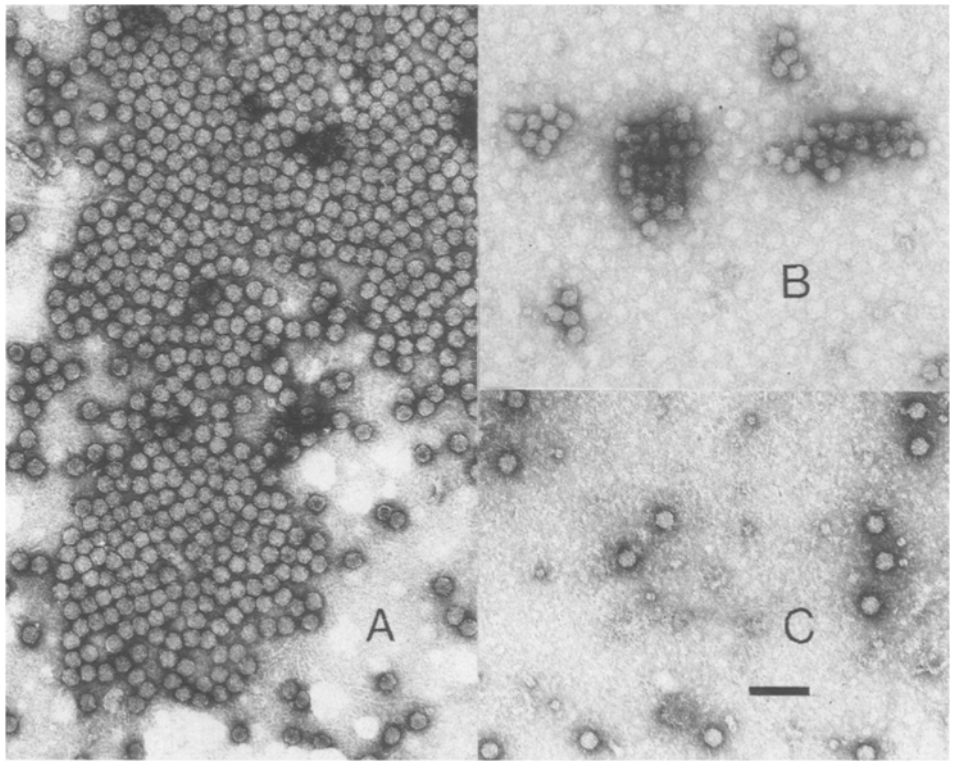

Fig. 4. Elektronenmicroscopische foto's van gedeeltelijk gezuiverd slavergelingsvirus. A) geconcentreerd onbehandeld preparaat. B) virus met antiserum tegen BWYV-USA (verdund 1 op 64) waarbij samenklontering optreedt, C) virus met antiserum tegen een niet verwant virus kersebladrolvirus (verdund 1 op 64) zonder samenklontering; de virusconcentraties waren in B en C gelijk. Vergrotingsstaaf geeft 100 nm weer.

Electron microscopy. Examination of purified preparations of BWYV revealed uniform isometric particles with a diameter of ca. 27 nm (Fig. 4).

Serology. The titre of BWYV antiserum to purified virus from lettuce was 512 in gel-diffusion tests. The reaction of purified virus with antiserum to BWYV (diluted 1:64) and with antiserum to an unrelated virus as a control (cherry leafroll virus, diluted 1:64) after 15 min of incubation is shown in Fig. 4B, C. The clumping of the purified virus produced by reaction with antiserum to BWYV is very clear when compared with the control preparation incubated with antiserum to cherry leafroll virus.

The infectivity of extracts of virus-infected leaves incubated with antiserum to BWYV (diluted 1:5) by Dr J. Duffus was completely neutralised but extracts incubated with buffer were highly infectious.

From the evidence of host range, electron microscopy and serology it was concluded that the virus isolated from lettuce was indeed a strain of BWYV.

2. *Comparison of indicators*

The results of the experiment to compare indicator species are summarised in Table 2. Considerable variability in symptom expression was recorded with *Ca. bursa-pastoris* (Fig. 5) and the biotype used in this experiment reacted only with very mild yellowing. Biotypes used subsequently have reacted more severely and in many cases with extreme stunting and reddening.

Table 2. Comparison of the suitability of five indicator plants for detection of BWYV.

Number of apterae of *Myzus persicae* used for inoculation	Intensity of symptoms on indicator plants, 3 weeks, and 5 weeks after inoculation									
	Senecio vulgaris		*Crambe abyssinica*		*Capsella bursa-pastoris*		*Claytonia perfoliata*		*Trifolium subterraneum*	
	3	5	3	5	3	5	3	5	3	5
Viruliferous 5	+[1]	+++[3]	++	+++	−	+	+	+	−	−
10	++[2]	+++	++	+++	−	+	+	++	−	−
15	+	++	++	+++	−	−	−	−	−	−
30	+++	+++	++	+++	+	++	+	+	±	−
Non viruliferous										
10	−	−	−	−	−	−	−	−	−	−
30	−	−	−	−	−	+	−	−	−	−

[1] mild symptoms; [2] moderate symptoms; [3] severe symptoms.

Tabel 2. Vergelijking van de geschiktheid van vijf indicatorplanten voor het aantonen van slavergelingsvirus.

Table 3. Reaction of lettuce cultivars exposed to natural infection with BWYV during 1977.

Cultivar	% showing symptoms	Cultivar	% showing symptoms
Attractie	18.9	Kagraner zomer	14.3
Auresta	34.0	Meikoningin	0.0
Avira	30.6	No. 7	24.6
Daresta	31.5	Reskia	4.5
Gallega de Invierno	48.7	Suzan	32.5
Groso	11.0	Type 91	60.0
Helresta	39.7	Virex	24.2
Hilde	21.3	Virilde	44.2
Hilde × Gallega	43.0	Viruzan	32.6
Irma	32.5	Zwart Duits	32.5

Tabel 3. Reactie van slacultivars na blootstelling aan natuurlijke infectie met het slavergelingsvirus in 1977.

Cr. abyssinica reacted most consistently and with very clear leaf reddening and downward rolling of leaf edges. In addition this species grew quickly from seed to give plants suitable for inoculation and was therefore selected as the best indicator for routine purposes.

Fig. 5. Range of symptoms in *Capsella bursa-pastoris* six weeks after inoculation with aphids with a lettuce isolate of BWYV (all plants are infected).

Fig. 5. Reeks van symptomen in Capsella bursa-pastoris zes weken na inoculatie met een sla-isolaat van het slavergelingsvirus met behulp van bladluizen (alle planten zijn geïnfecteerd).

3. Incidence of BWYV in lettuce and other hosts

During the summer of 1977 BWYV was detected in all of fifteen experimental and commercial plantings of lettuce inspected in the provinces North-Brabant, North-Holland, South-Holland and Limburg. Incidence was usually low (one to two per cent) although in one experimental crop an incidence of 17% was observed. In 1978, following a cool damp spring with very small populations of aphids, BWYV was detected at a very low level (less than 1%) and only in crops surveyed in September.

BWYV was also isolated from the following naturally infected plants (number of positives/number of plants tested): *Ci. endivium* (8/10), *Ci. intybus* (witloof chicory) (3/5), *Spinacia oleracea* (3/3), *Ca. bursa-pastoris* (13/15), *Senecio vulgaris* (10/15), but not from *Stellaria media* (0/15) or *Chenopodium album* (0/15) growing in the same areas. The witloof samples were from the crop that upon visual inspection later during 1978 showed ca. 50% infection (Fig. 3). In such plants the virus could again be readily detected with *M. persicae* on *Cr. abyssinica.* Infected *Senecio* plants usually showed a striking reddening, especially of the lower leaves.

4. Reaction of lettuce cultivars

The incidence of symptoms of natural infection with BWYV of 20 lettuce cultivars grown at Lienden during 1977 is shown in Table 3. The average incidence was considerably higher than that observed in commercial plantings, probably because the experiment was assessed at a later date after planting than that at which commercial crops are harvested. 'Meikoningin' and 'Reskia' showed a very low incidence of symptom development and both cultivars were tested by inoculation of BWYV in the glasshouse. Under these conditions both were completely susceptible and thus the low field incidence was possibly due to either aphid avoidance or delayed symptom expression.

The following species and cultivars of *Cichorium* and *Lactuca* were tested for resistance to BWYV during 1978: *Ci. endivia* 'Breedblad Volhart Winter' and 'Nummer Vijf'; *Ci. intybus* 'Groenlof IVT'; *L. sativa* var. *acephala* 'Amerikaanse Roodrand' and 'Australische Gele'; *L. sativa* var. *capitata* 'Gallega de Invierno', 'Great Lakes 21', 'Hilde', 'Hilde × Gallega', 'H 138', 'Meikoningin', 'No 91', 'Valmaine' and 'Zwart Duits'; *L. sativa* var. *capitata* × *L. serriola* 'Hilde × Botanische'; *L. sativa* var. *longifolia* 'Snijsla No. 1' and 'Snijsla No. 2'; *L. serriola* '681', '702' and '717' and *L. virosa.* No natural infection was observed which was consistent with the sporadic and low level of infection detected in other crops. Of the plants inoculated, however, all except *Ci. intybus* 'Groenlof IVT' showed distinct symptoms of infection. *L. serriola* '702' and '717' showed a striking leaf reddening instead of chlorosis.

Discussion

Duffus (1977) pointed out that BWYV has an extremely wide host range and is serologically related to a number of yellows viruses including *Malva* yellows virus, turnip yellows virus, beet mild yellowing virus, RPV isolate of barley yellow dwarf

virus, and two strains, SDV-DS and SDV-Y, of soybean dwarf virus. All of these viruses have some hosts in common and the first three listed above have very similar host ranges. Duffus (1964) showed that considerable host-range variation can occur even between what he considered were strains of BWYV. Some of the strains which he described did not infect *Beta vulgaris* and in this respect resemble the European strains of BWYV. It seems probable that the viruses which are serologically related to BWYV arose from a common stock. Since these viruses are transmitted only by aphid vectors and in a persistent manner it is likely that strains have arisen by host/vector selection and adaptation. The possibility of heterologous encapsidation as outlined by Rochow (1972) could also be responsible for the development of different strains of BWYV.

In studies with the aim to determine whether a yellows disease of a particular crop is caused by a member of the BWYV group it is sufficient to use one or more of the diagnostic hosts listed by Duffus (1972). These are *Ca. bursa-pastoris, S. vulgaris,* and *Cl. perfoliata* which react to all isolates tested. Obviously, when investigating the relationship of a BWYV isolate to other reported strains it is necessary to use a more extensive host range. When isolating BWYV from hosts other than the crop being studied, the isolates obtained should also be checked for pathogenicity to that crop. For example when isolating from weed hosts to determine the origin of BWYV infecting lettuce one should transmit first to lettuce and then to one of the diagnostic hosts if symptoms are not clear. In this way spurious results due to, for example beet mild yellowing virus, can be avoided.

Some workers (Russell, 1965; Nagi, 1975) have reported problems with one or the other of the diagnostic indicators (Duffes, 1972) due to unspecific reactions under artificial illumination. We have experienced that additional illumonation is necessary to produce rapid and distinct symptoms in infected plants.

We have now proved the virus isolates from lettuce, chicory witloof and endive to be a strain of BWYV that does not infect beets. This was done by host-range tests and was convincingly corroborated by serology and electron microscopy. This paper is the first report on the occurrence of BWYV in the Netherlands.

BWYV seems to be of minor economic significance to lettuce growing in the Netherlands in most years. Since in this country lettuces are planted and not directly sown, the crop is normally harvested within four to six weeks of planting. It is probable that many infected plants are harvested before symptoms appear. However, detailed observations over a number of seasons may well show that this disease is important since at present the symptoms caused by BWYV are often attributed to other causes, especially nutritional imbalance. In the USA and in Britain, BWYV is considered of considerable economic importance and it would be advantageous for seed companies in the Netherlands to incorporate resistance to BWYV in their lettuce cultivars. Watts (1975) reported no evidence of immunity to BWYV in 70 cultivars and in over 500 lines from ten crosses. This agrees with our results which also show the high susceptibility to BWYV of *L. serriola, L. virosa* and *L. sativa* 'Gallega de Invierno' which are often used in breeding because of their resistance to lettuce mosaic virus.

Natural infection of *Ci. endivia* (endive) and of *Ci. intybus* (witloof chicory) causes very clear yellowing and in endive also a severe stunting. BWYV is potentially a serious problem in these crops. It is interesting that BWYV produces clear symp-

toms in witloof chicory but that the 'groenlof' type tested by inoculation remained symptomless. This possible source of resistance should be further investigated.

Samenvatting

Vergeling van sla en enkele andere groentegewassen in Nederland door het slavergelingsvirus

Reeds gedurende enkele jaren trekt in Nederland een vergelingsziekte van sla (Fig. 1 en 2) de aandacht. In 1977 en 1978 werd de ziekte nader bestudeerd en ook waargenomen in andijvie, witlof (Fig. 3) en spinazie. Uit zieke planten van deze vier gewassen en uit de onkruiden herderstasje en kruiskruid, groeiend in de buurt van de zieke sla, kon door *Myzus persicae* op persistente wijze een virus worden overgebracht. Het werd op grond van zijn waardplantenreeks (Tabel 1), deeltjesmorfologie (Fig. 4A) en serologie (Fig. 4B) herkend als het in de USA beschreven 'beet western yellows virus' (BWYV).

Het Nederlandse virus komt overeen met in andere landen gerapporteerde Europese isolaten van het virus, maar verschilt van Amerikaanse doordat het niet in staat is om biet, chinese kool en radijs te infecteren. Daarom is voor het virus door Bos en Ashby (1978) de Nederlandse naam slavergelingsvirus ingevoerd. De meest geschikte indicatorplant voor routinetoetsing is *Cramble abyssinica* (Tabel 2). De reactie van herderstasje varieert al naar individu van nagenoeg letaal tot vrijwel symptoomloos (Fig. 5).

In gedeeltelijk gezuiverde preparaten bleken de deeltjes bolvormig te zijn en ca. 27 nm in diameter (Fig. 4A). Zulke preparaten reageerden met antiserum tegen een Amerikaanse stam van het virus (BWYV) in toetsen die gebruik maken van infectieneutralisering, gel-diffusie en serologisch-speciefieke elektronenmikroskopie. Bij laatstgenoemde techniek werd een fraaie deeltjesklontering waargenomen (Fig. 4B), die ontbrak na incubatie van gezuiverd virus met een antiserum tegen het niet verwante kersebladrolvirus (Fig. 4C).

Bij veldwaarneming in 1977 van 20 slarassen, waarbij tot 60% van de planten van één ras werden aangetast, bleken twee rassen niet of weinig vatbaar (Tabel 3). Bij inoculatie in de kas bleken ze echter volledig vatbaar. In 1978 werd een aantal soorten en rassen van *Cichorium* en *Lactuca* blootgesteld aan natuurlijke en aan kunstmatige infectie. Behalve *C. intybus* 'Groenlof IVT' waren allen vatbaar, ook *L. sativa* 'Gallega de Invierno', *L. serriola* en *L. virosa*.

Het virus lijkt algemeen voor te komen. Meestal is de infectiegraad niet hoog. Vanwege de lange incubatieduur in sla is het virus in dat gewas bij de hier toegepaste teeltwijze waarschijnlijk van geringe betekenis. Het lijkt echter een potentieel belangrijk pathogeen voor andijvie en witlof.

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