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Coriander Feathery Red-Vein Virus, a Propagative Plant Rhabdovirus, and its Transmission by the Aphid *Hyadaphis foeniculi* Passerini

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Coriander feathery red-vein virus, an aphid-borne, propagative, plant rhabdovirus causing distinct symptoms on coriander, *Coriandrum sativa* and transmitted by the honeysuckle aphid, *Hyadaphis foeniculi* is described. The virus was isolated in coriander from naturally infective aphids collected on symptomless parsnip *(Pastinaca sativa)*. Coated bacilliform particles, about 75 × 216 nm were found in infected coriander tissue, most often enclosed within invaginated nuclear cisternae.

Coriander, celery *(Apium graveolens), Nicotiana glutinosa, N. clevelandi* and their hybrid developed symptoms after aphid inoculation. Once infected, the virus could be moved among the tobacco species by mechanical inoculation. In addition to parsnip, chervil *(Anthriscus sylvestris),* water hemlock (*Cicuta* sp.), carrot *(Daucus carota*), fennel *(Foeniculum vulgare)* and parsley *(Petroselinum crispum)* were found to be symptomless hosts.

Hyadaphis foeniculi, among twelve aphid species tested, was the only consistent vector.

An examination of the vector-virus relationships indicated acquisition could occur within 2 hours and after a 8.5-day (at 25 C), dosage-sensitive, median latent period, inoculation could take place within 15 to 30 minutes. Insects could remain infective for life, but the mean weighted transmission period ranged from 13 to 20 days. Transovarial passage occurred, with a maternal rate of about 55 percent, and a filial rate of 3 to 10 percent. Five successive serial passages of the virus by injection, with a maintenance of titer, indicated the virus replicated in *H. foeniculi.* Neither longevity nor the reproductive capacity of the aphid vector appeared to be effected by the infection.

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INTRODUCTION

WHILE TESTING POTENTIAL VECTORS AND HOSTS for a suspected carrot motley dwarf virus in July, 1976, honeysuckle aphids (*Hyadaphis foeniculi* Passerini) were collected from apparently healthy parsnip (*Pastinaca sativa* L.) in a garden at the University of California Gill Tract, Albany. The insects were transferred to a series of test plant species, including coriander (*Coriandrum sativum* L.). Some of the coriander plants developed red vein-banding symptoms, suggesting possible viral infection.

An electron microscopic examination of a negatively stained leaf-dip preparation revealed the presence of bullet-shaped rhabdovirus-like particles.

Coriander belongs to the plant family Umbelliferae, and a survey of the literature showed that at least 20 viruses have been associated with umbelliferous plants (Tomlinson and Carter, 1970; Wolf and Schmelzer, 1972; Zitter, 1975). Most are sap transmissible with isometric or flexuous filamentous particles, and commonly vectored by the yellow willow aphid, *Cavariella aegopodii* (Scop.). However, rhabdovirus-like particles were associated with a disease of cow parsnip (*Heracleum spondylium* L. *australe* (Hartm.) Ahlfv) (Polák, Králík, and Limberk, 1977), with a carrot motley dwarf complex in parsley (*Petroselinum crispum* Nym.) (Tomlinson and Webb, 1974), and with a latent virus in carrot (*Daucus carota* L.) in Japan (Ohki, Doi, and Yora, 1978).

The rhabdovirus infecting cow parsnip was reported to cause mild chlorosis or flavescence in the first leaf, followed by deformation and a bright yellow flecking discoloration expanding from the center of the lamina along the main vein. The virus was sap transmissible to a number of herbaceous hosts including parsley (Polák, 1966), and the bacilliform particles measured 90 × 265 nm in thin sections of naturally infected cow parsnip or in leaves and lower petals of juice inoculated parsley (Polák, Králík, and Limberk, 1977). No vector was reported.

Another rhabdovirus, found to be widespread in parsley crops in Worcestershire, England, was associated with severe symptoms of carrot motley dwarf infection, including reddish or yellowish leaf discoloration and extreme plant stunting (Tomlinson and Webb, 1974). Mechanically inoculated *Nicotiana clevelandii* Gray developed atypical symptoms. Electron microscopic examination of negatively-stained leaf homogenates of parsley and *N. clevelandii* showed rhabdovirus-like particles measuring 87 × 214 nm. *Cavariella aegopodii* was reported to be the vector (Martelli and Russo, 1977), but details on transmission are not available.

Finally, a rhabdovirus, 70 to 75 × 220 to 240 nm, was found in apparently healthy carrots in Japan. It was transmitted by aphids (*Semiaphis heraclei* Takahashi) to some Umbelliferae, including carrot, celery (*Apium graveolens* L.) and *Cryptotaenia japonica* Hassk. Infected plants exhibited vein-clearing 15 to 20 days after inoculation but later

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became symptomless. The virus was not juice transmissible. Vector relationships included an acquisition threshold period of two hours, a 9 to 12-day latent period, and retention of inoculativity for at least 12 days. The virions were labile in that only nucleocapsids could be found in negatively-stained dip preparations (Ohki, Doi, and Yora, 1978).

Aphids are reported to transmit at least six plant rhabdoviruses, and the following work was undertaken to investigate the host range and vector-virus relationships of this disease, and its similarity or differences to those other rhabdovirus diseases reported to affect umbelliferous plants (Tomlinson and Webb, 1974; Polák, Králík, and Limberk, 1977; Ohki, Doi, and Yora, 1978).

MATERIALS AND METHODS

Virus

Coriander feathery red-vein virus, after its original isolation in the coriander fed upon by field collected *H. foeniculi,* has been maintained in the greenhouse by constant transfers of infective aphids to coriander test plants.

Aphids

Nonviruliferous *H. foeniculi* colonies were initiated by allowing five viviparous, parthenogenetic apterae from a single clone to larviposit on young 5-leaf stage celery, or coriander, for 24 hours. The apterae were removed and the larvae were allowed to mature on these plants. Groups of five aphids were then moved at 24-hour intervals to five to 20 new test plants, depending on need. The larvae deposited on each set of plants were allowed to mature before repeating the cycle. Thus, equal age cohorts of aphids ranging from 1-day-old larvae to mature apterae were available for experiments throughout the study. Rearing of aphids, unless otherwise stated, was done in a 21 C growth chamber with a 9000 lux, 14-hour photophase and 10-hour dark phase. None of the coriander plants upon which noninfective colonies were initiated developed symptoms of the disease.

Viruliferous aphids usually were maintained by confining adult apterous viviparae to virus-source plants using butyrate-acetate cylindrical cages closed at the top with organdy cloth. Caged plants were kept in a growth chamber set at 25 C with constant light. After 24 hours, the adults were removed and the larvae were allowed to continue the acquisition access period (AAP) until used. Fresh virus-source plants were used each time a viruliferous colony was needed.

Test plants

All transmission tests, with the exception of host range, were made from and to young coriander. Seeds were germinated in clay seed-pans containing vermiculate, and transplanted at the cotyledon stage into 5 cm plastic pots containing a mixture of fine river sand and peat moss. Test seedlings usually were used in the early cotyledon stage within 4 to 6 days of germination. At least one of the daily greenhouse-waterings during 5 days of each week was with nutrient solution.

Transmission tests

Unless otherwise stated, transmission was by single apterae acquiring virus by feeding or by being injected with inoculum derived from infectious aphid-head extracts (Sylvester and Richardson, 1971). Insects were confined to test plants using cellulose-butyrate (or nitrate) cages covered at one end with fine nylon mesh or organdy cloth. Aphids were transferred using a microaspirator. Most transmission tests were done in growth chambers maintained at approximately 25 C with constant light. Detailed methods used in specific experiments are given in the "results" section.

After removal of test aphids, the plants were fumigated with nicotine or sprayed with a persistent insecticide (Guthion) prior to being placed in the greenhouse. Test plants were observed for symptom development for at least 30 days before being discarded or used as virus sources.

Plants on which nonviruliferous aphids had been similarly confined usually were used as controls. Occasionally, plants on which healthy stock aphids were reared were fumigated and observed for symptoms. None developed symptoms, and it was assumed that stock colonies were nonviruliferous.

Aphid injection

Inoculum was prepared from aphids fed on infected plants for at least 5 days. The injection technique followed that described by Sylvester and Richardson (1971) viz., an adult aphid, or last instar larva, from a diseased plant, was surface sterilized by dipping in 70 to 95 percent ethanol. The head was detached and triturated in a sterile depression slide using the tip of a micropipette filled with 5 lambda of cold distilled water. The resulting inoculum was mixed by moving it in and out of the micropipette at least twice, then finally sucked into the micropipette and put in a refrigerator.

Remains of the head were then mixed with 1 percent sodium phosphotungstate, pH 6.8, put on a Formvar-coated grid, and examined for virus particles using a Philips EM 200 electron microscope. If positive, the inoculum was used for injection.

Injection was done using glass needles. Recipient aphids usually were starved for at least 1 to 2 hours in a refrigerator (or sometimes at room temperature) before injection to reduce bleeding and to aid in settling on the test plants (Muller, 1965).

Small drops of inoculum were placed on a Parafilm covered dish of ice across which an extra strip of Parafilm, anchored on each side by strips of masking tape, had been placed. Recipients, anaesthetized with a stream of moist CO_2, were injected in the dorsal abdominal cavity somewhat anterior to the siphunculi.

After injection, aphids were allowed to recover in a tightly closed container before being caged on test plants. Usually they were initially caged in lots of five per test plant. Survival was checked for the first 2 days, after which surviving insects were individually caged and subsequently transferred every 24 to 48 hours to new sets of test plants.

Bioassay

Median latent periods (LP_{50}) (Sylvester, 1965) were estimated by calculating a least squares regression on time of a log-probit transformation of cumulative 1st transmissions. To simplify the calculations, inoculation of test plants was assumed to have occurred

at the mid point of each transfer interval.

Karber's method (Karber, 1931) in which

$$LP_{50} = \tfrac{1}{2} \sum (P_{i+1} - P_i)\ (X_{i+1} + X_i)$$

was used to estimate an LP_{50} when less than four transmission values were available, or when the rate of transmission was 10 percent or less. In the formula, P is the proportion of insects transmitting for the first time at time X, with X being the midpoint of the transfer interval. The summation is done over k intervals, in which, $P_1 = 0$ and $P_k = 1.0$.

Electron microscopy

Thin sections of plant material, both diseased and healthy, were prepared by cutting discs, 1 to 2 mm in diameter, from coriander leaves. These were fixed for 2 hours in cold glutaraldehyde in 0.1 M cacodylate buffer, pH 7.2, rinsed overnight in cold buffer and postfixed 1 hour in cold 1 percent osmium tetroxide. The tissue was dehydrated in a graded ethyl alcohol-propylene oxide series and embedded in Spurr's low viscosity epoxy resin embedding medium (Spurr, 1969). Sections were cut on a Porter Blum MT 2 Ultramicrotome with a diamond knife, stained with uranyl acetate and lead citrate (Reynolds, 1963), and examined in a Philips EM 200 electron microscope. Aphid head-dips (Sylvester and Richardson, 1971) and leaf dips were negatively stained using 1 percent sodium phosphotungstate, pH 6.8, or saturated uranyl acetate in 50 percent alcohol.

Plant host range

By vectors. Apterous viviparae were allowed to larviposit on infected coriander plants for 24 hours at 25 C and constant light. Maternal apterae then were removed and the larvae left a minimum of 7 and a maximum of 10 days before being transferred to healthy candidate-host test plants. After a variable inoculation access period (IAP) of 24 to 72 hours at 25 C and constant light, the plants were fumigated with nicotine, put in the greenhouse and observed for symptom development for at least 30 days. Variations on this basic plan are noted in the results section.

By mechanical inoculation. Crude sap-extracts were prepared by triturating aphid-infected coriander, *Nicotiana clevelandii* or *N. glutinosa* tissues in 0.05 M phosphate buffer, pH 7.0 and squeezing the pulp through double-layered cheese cloth.

Leaves of test plants were dusted with 400-mesh celite before applying inoculum with a finger or with a Q-tip cotton swab. Inoculated leaves were immediately rinsed with tap water. All test plants were grown in 7.62 or 12.7 cm diameter plastic or clay pots. Control plants were treated similarly using buffer only and were maintained under the same greenhouse conditions.

Vector range

Nonviruliferous candidate species of aphids were allowed an AAP, usually of 7 days, on infected coriander and then transferred individually or in lots of two or more aphids to healthy coriander test plants. The IAP varied from 7 to 11 days, but the total time from the beginning of the AAP to the end of the IAP was never less than 8 days.

RESULTS

Plant host range by vector tests

Hyadaphis foeniculi was used in limited trials to determine if parsnip was a symptomless host and if other plants, especially members of the family Umbelliferae, were susceptible to the virus by aphid transmission.

Parsnip as a symptomless host

Procedure. Larvae born during a maternal access period of 24 hours at 25 C were allowed a 10-day AAP before being caged in lots of five on each of 30 healthy cotyledon-stage parsnip test plants. The lots were moved serially to six sets of test plants using the following sequence: parsnip, coriander, parsnip, coriander, parsnip, parsnip. The IAPs were 1 or 2 days on coriander and 2 or 3 days on parsnip. The parsnips came from seeds of the original plant where CFRVV-infective aphids were collected. Five control plants, each with five to eight nonviruliferous aphids, were used at each transfer.

Recovery tests to coriander or to *Nicotiana clevelandii* were made from 30 parsnips of the first and third set of transfers. Virus-free larvae were given an 11-day AAP, and then four lots of five to seven aphids from each plant were caged on individual coriander test seedlings. The lots of aphids subsequently were transferred to an additional three sets of coriander test plants at 2- to 3-day intervals.

The last two sets of parsnip plants also were tested. Virus-free larvae were given an 8-day AAP, and then individual coriander test plants were mass inoculated using 40 to 50 aphids from each candidate parsnip of the third set. Twenty-seven parsnips of the 4th set were similarly tested, using *Nicotiana clevelandii* as the assay host.

Results. Virus symptoms did not develop in any of the parsnips, although recovery tests to coriander demonstrated plants in each series were infected (Table 1).

TABLE 1
PARSNIP, *PASTINACA SATIVA* AS A SYMPTOMLESS HOST OF CORIANDER FEATHERY RED-VEIN VIRUS*

Serial transfer	Test host	Assay		Control
		Test series	Recovery series	
1	Parsnip	0/30	53/120	0/10
2	Coriander	23/30	—	0/5
3	Parsnip	0/30	45/120	0/10
4	Coriander	24/30	—	0/5
5	Parsnip	0/30	19/30	0/10
6	Parsnip	0/30	24/27	0/10

*The numerators above are the number of plants developing visual symptoms; denominators are the number tested. In the recovery series, tested parsnips were used as virus source plants and test plants were coriander, *Coriandrum sativum*.

Other host plant tests

Eighteen species, from five plant families including the Umbelliferae, were tested, using aphid vectors, as possible hosts of CFRVV. Table 2 shows the results. Only celery, *N. clevelandii, N. glutinosa,* and their hybrid developed symptoms.

TABLE 2.
PLANT HOST RANGE TESTS OF CORIANDER FEATHERY RED-VEIN VIRUS USING *HYADAPHIS FOENICULI* AS APHID VECTORS

Family	Species	Result	
		Initial test	Recovery test
Compositae	*Lactuca sativa* L.	0/90*	—
	Sonchus oleraceus L.	0/10	—
Geraniaceae	*Erodium cicutarium* L. (L'Her.)	0/10	—
Rosaceae	*Fragaria vesca* L.	0/10	—
Solanaceae	*Nicotiana clevelandii*	51/57	—
	N. glutinosa L.	11/20	—
	N. glutinosa x *N. clevelandii* (hybrid)	18/25	—
	N. tabacum L.	0/10	—
	Physalis floridana Rydb.	0/15	—
Umbelliferae	*Anethum graveolens* L.	0/15	—
	Anthriscus sylvestris L.	0/10	2/30
	Apium graveolens L.	15/40	—
	Cicuta sp.	0/15	9/28
	Conium maculatum L.	0/150	—
	Daucus carota L., var. sativa DC.	0/10	27/40
	Foeniculum vulgare Mill.	0/20	3/32
	Heracleum lanatum Michx.	0/15	—
	Petroselinum crispum Nym.		
	cv: Hamburg thick-rooted	0/60	29/62
	Plain or Hardy Italian	0/60	13/50
	Plain or Single	0/10	4/14
	Moss Curled	0/10	0/23
	Dark Moss Curled	0/60	18/57

*The numerators above are the number of plants showing symptoms; the denominators are the number tested. Groups of infective aphids were given a minimum of 24-hr access to candidate test plants. Percentage of insects alive at end of test ranged from 64% to 94% on umbelliferous hosts, and 0% to 13% on Solanaceae. Survival records were not kept in tests with *Erodium cicutarium, Fragaria vesca,* or *Lactucae sativa.* In tests with *Sonchus oleraceous,* 34% of the aphids survived. Recovery tests, made in selected instances, used *H. foeniculi* as vectors and coriander, *Coriandrum sativum* as the assay host.

Hyadaphis foeniculi did not survive well on non-umbelliferous hosts tested (Table 2). However, poor survival on susceptible host plants does not necessarily result in a failure of transmission to occur, e.g., transmission of LNYV occurs on both lettuce and tobacco (Stubbs and Grogan, 1963) poor hosts of the vector *H. lactucae* (Stubbs and Grogan, 1963; Eastop, 1958; Hille Ris Lambers, 1949). In any event, none of the non-umbelliferous hosts developed symptoms in our tests.

Of nine umbelliferous plant species tested, other than coriander, only celery developed symptoms. Recovery tests made from chervil (*Anthriscus sylvestris* L.), water hemlock (*Cicuta* sp.), carrot, fennel (*Foeniculum vulgare* Mill.), parsnip and parsley indicated all were symptomless hosts (Table 2). No symptoms developed on dill

(Anethum graveolens L.), poison hemlock (*Conium maculatum* L.), or cow parsnip, but since no recovery tests were made from these species, their susceptibility is uncertain. Lack of symptom expression in many of the umbelliferous hosts may account for the disease being unnoticed previously.

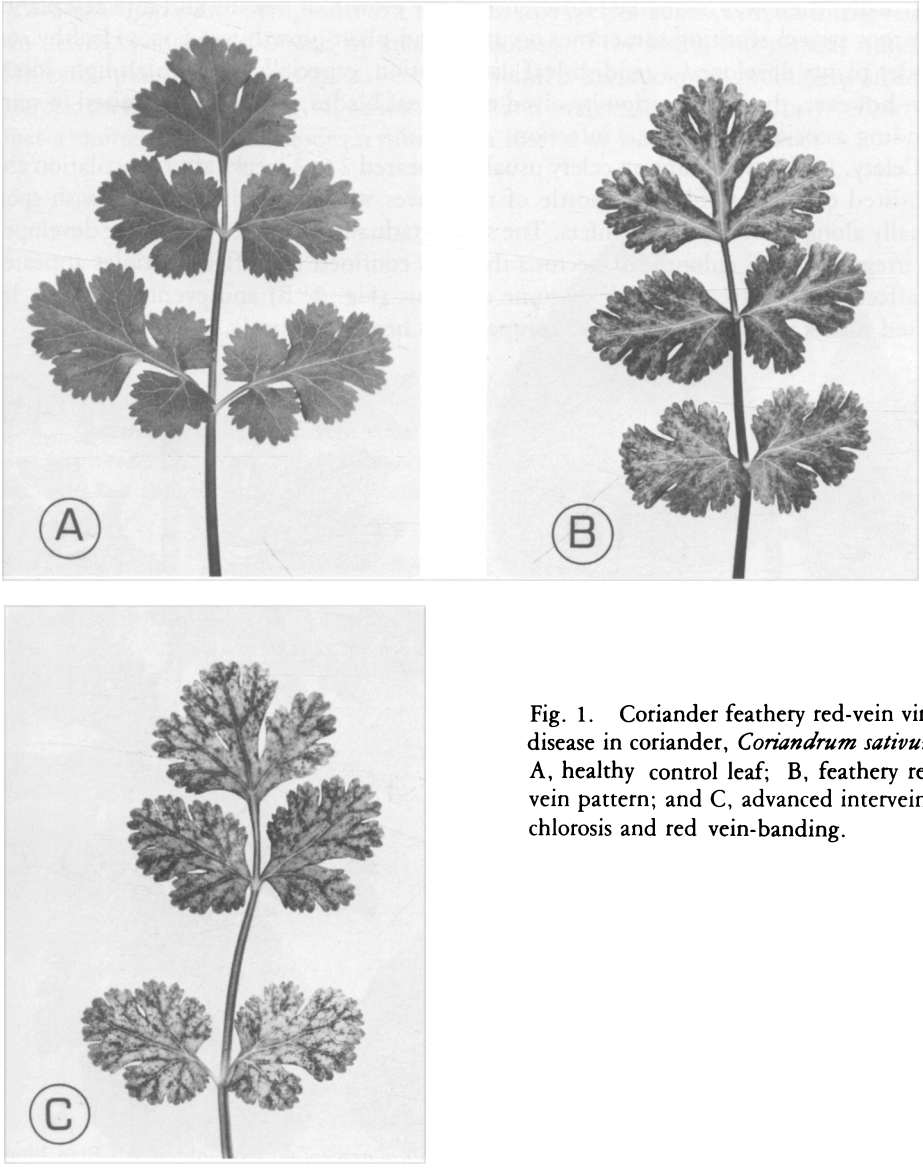

Fig. 1. Coriander feathery red-vein virus disease in coriander, *Coriandrum sativum*. A, healthy control leaf; B, feathery red-vein pattern; and C, advanced interveinal chlorosis and red vein-banding.

Symptomatology

Coriander. Early symptoms of CFRVV disease in coriander were faint chlorotic vein-banding followed by an increasing prominence of veins and veinlets. Leaflets could be mildly chlorotic with a smooth and glassy appearance. Necrotic flecks or streaks developed and permeated interveinal tissues along the veins and veinlets. Affected veins

and veinlets gradually turned red or reddish brown, resulting in a feathery pattern (Fig. 1, B). The discoloration gradually progressed centrally from the margins towards the petiole. Interveinal tissues may have paled, but the veins remained characteristically red-banded (Fig. 1, C).

Usually, there was no marked difference in the growth of healthy and infected plants, but root system stunting sometimes occurred and plant growth was poor. Healthy coriander plants developed a reddish leaf discoloration, especially under high light intensity; however, the discoloration involved entire leaf blades, and was not limited to vein-banding associated with virus infection.

Celery. Initial symptoms on celery usually appeared 2 to 3 weeks after inoculation and consisted of a faint chlorotic mottle of the leaves with fairly discrete yellowish spots usually along the veins and veinlets. The spots gradually elongated and there developed an irregular veinal chlorosis or necrosis that was confined to leaflets. Petioles appeared unaffected but leaves gradually become chlorotic (Fig. 2, B) and eventually died. Infected plants usually were stunted compared to healthy controls.

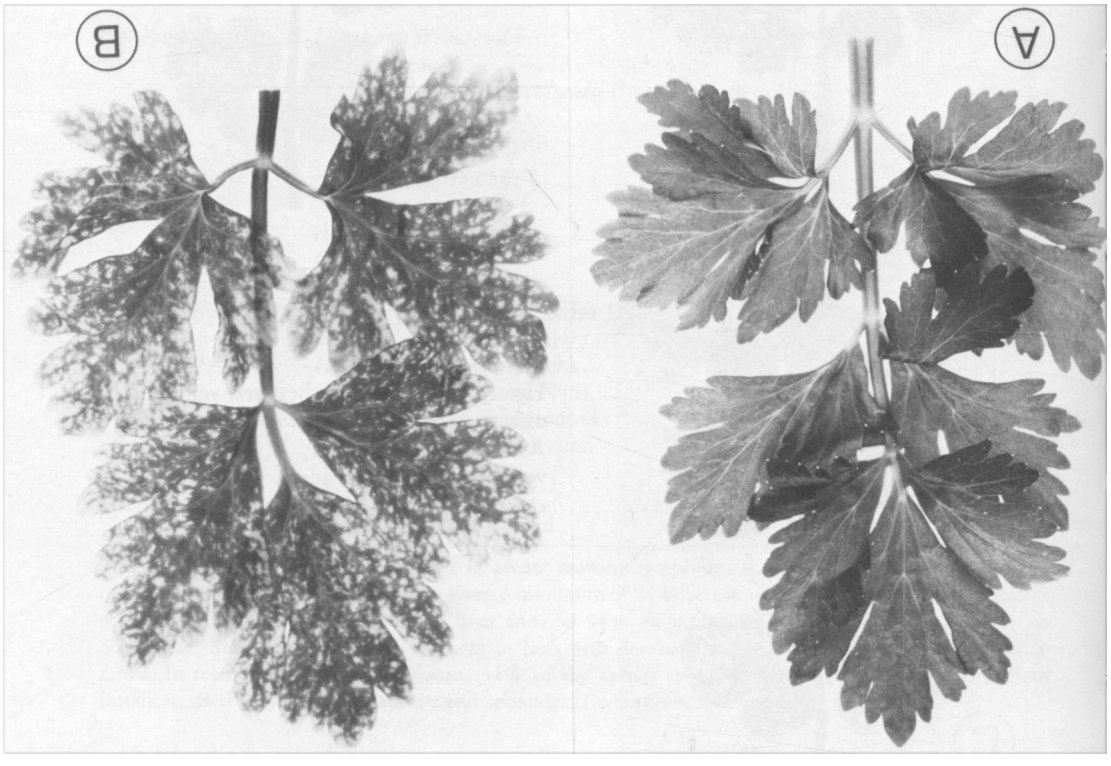

Fig. 2. Coriander feathery red-vein virus in celery, *Apium graveolens,* cv. Golden Self-Blanching. A, healthy control leaf; B, leaf with advanced yellow chlorotic leaf-spotting.

***Nicotiana clevelandii* and *clevelandii* x *glutinosa* hybrid.** Visible symptoms on *N. clevelandii* and their hybrid, first appeared about 10 to 14 days after inoculation, as a mild veinal chlorosis of young, developing leaves (Fig. 3, right). Symptoms initially were most pronounced around leaf margins, but later spread to cover the entire leaf. Veinlets gradually became severely chlorotic and clear. Interveinal tissue remained green, resulting in a severe chlorotic netting pattern on mature leaves. Some infected

leaves were slightly narrower and at times puckered, twisted or cupped. A general distortion and stunting occurred and, depending on severity, infected plants had fewer and smaller flowers than did healthy controls. As leaves aged, the vein clearing became less prominent, and occasionally symptom remission occurred.

Nicotiana glutinosa. Symptoms of CFRVV in this species began with an initial raised vein-netting symptom followed by gradual chlorosis of the leaves and general stunting of infected plants. As plants aged, veins and veinlets became more prominent and the chlorotic areas increased (Fig. 4, center, right) and eventually turned a rusty yellow. At times a shortening of internodes resulted in a rosette of leaves at terminals.

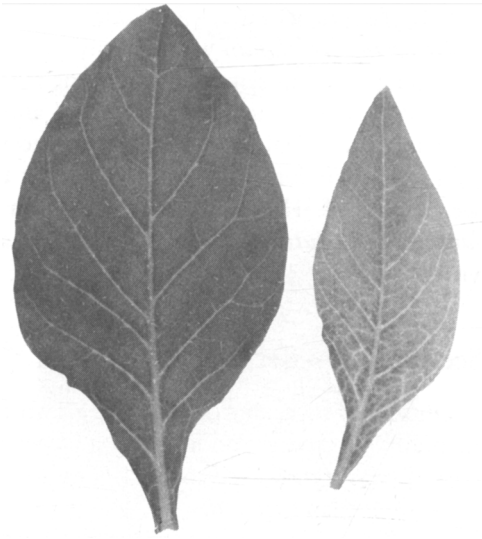

Fig. 3. Coriander feathery red-vein virus in *Nicotiana clevelandii.* Left, healthy control leaf; right, leaf showing mild veinal chlorosis.

Fig. 4. Coriander feathery red-vein virus in *Nicotiana glutinosa.* Left, healthy control leaf; right and center, leaves with interveinal chlorosis and vein-netting symptoms, respectively.

Plant host range by mechanical inoculation

The following plant species were tested for susceptibility to CFRVV by sap inoculation: Amaranthaceae—*Gomphrena globosa* L.; Chenopodiaceae—*Chenopodium amaranticolor* Coste & Reyn., *C. quinoa* Willd.; Compositae—lettuce (*Lactuca sativa* L.), sowthistle (*Sonchus oleraceus* L.); Cucurbitaceae—cucumber (*Cucumis sativus* L.); Leguminosae—kidney bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* L.); Plantaginaceae—plantago (*Plantago major* L.); Solanaceae—pepper (*Capsicum frutescens* L.), jimson-weed (*Datura stramonium* L.), tomato (*Lycopersicon esculentum* Mill.), *Nicotiana clevelandii* Gray, *N. glutinosa* L., *N. glutinosa* x *N. clevelandii* hybrid, *N. tabacum* L. var. White Burley, petunia (*Petunia hybrida* Vilm.); Umbelliferae—carrot, celery, coriander, cow parsnip, parsley, parsnip, and poison hemlock.

Nicotiana clevelandii was the only species, out of the 24 tested in the eight families, to develop systemic symptoms following mechanical inoculation using juice from infected coriander. This occurred in one trial, and 3 out of 10 test plants developed a faint systemic interveinal chlorosis. Neither recovery tests nor electron microscopic examination were done for confirmation. In other trials, involving 35 test plants, no symptoms were observed. However, using inoculum prepared from aphid-inoculated *N. clevelandii* or *N. glutinosa,* both these species and their hybrid were susceptible with trials yielding 11/15, 3/15 and 3/10 infections, respectively.

Seed and dodder transmission

On several occasions plants were grown from samples of seed, collected from experimentally infected coriander and *N. clevelandii* plants. There was no evidence that the CFRVV was transmitted through seed to the more than 1000 coriander or the 100 *N. clevelandii* plants grown.

Five CFRVV-infected coriander plants were infested with dodder, *Cuscuta campestris* Yunkers, and linked with 25 coriander test plants. There was no evidence of virus transmission.

Particle morphology and electron microscopy

Bullet-shaped particles typical of phosphotungstic acid (PTA), negatively-stained rhabdovirus preparations were found in viruliferous aphid head-dips and CFRVV-infected plant dips (Fig. 5A, B). There was no obvious difference in the appearance of the preparations from either source. Uncoated nucleocapsids appearing as transversely striated helical cylinders (Fig. 6A, B) were common, frequently more numerous than were bullet-shaped forms. Particles with the helix uncoiling at the broken ends were observed (Fig. 7).

Nucleocapsids occasionally appeared to lie side by side, sharing a common outer protein coat (Fig. 8). This may have resulted from a fusion of viral envelopes of individual particles or co-maturation of closely appressed nucleocapsids.

Thin sections of infected coriander leaves showed aggregates of bacilliform particles, predominately in nuclei. Particles were coated and uncoated, often in periniuclear cisternae (Fig. 9). Other variations found with CFRVV virions in leaf tissue included encapsulated particles in nuclei (Fig. 10). Virus-like particles occasionally were found in cytoplasm, and while not in aggregates as usually seen in nuclei, groups did occur in tubular cisternae (Fig. 11).

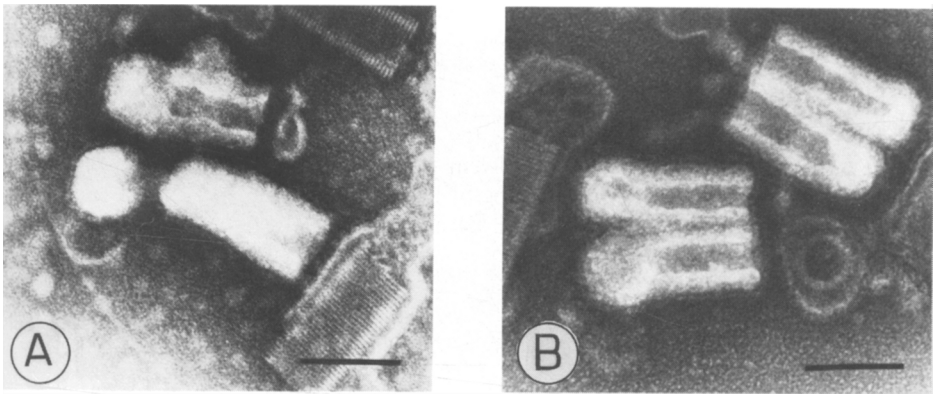

Fig. 5. Coriander feathery red-vein virus particles negatively stained with phosphotungstic acid, from an infected aphid *Hyadaphis foeniculi* (A), and infected coriander, *Coriandrum sativum* (B). Bars represent 100 nm.

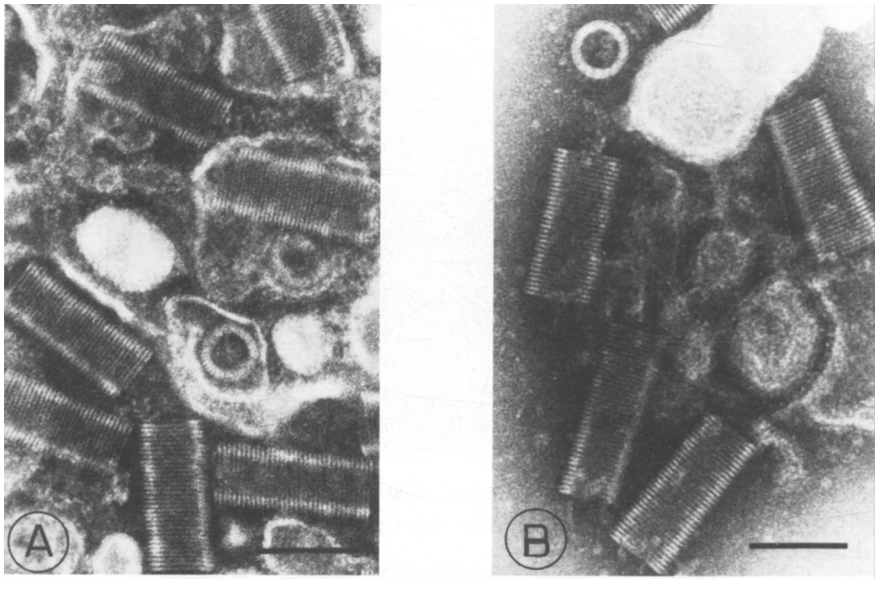

Fig. 6. Coriander feathery red-vein virus particles negatively stained with phosphotungstic acid, showing uncoated helical nucleocapsids in longitudinal and cross section from the aphid, *Hyadaphis foeniculi* (A) and coriander, *Coriandrum sativum* (B). Bars represent 100 nm.

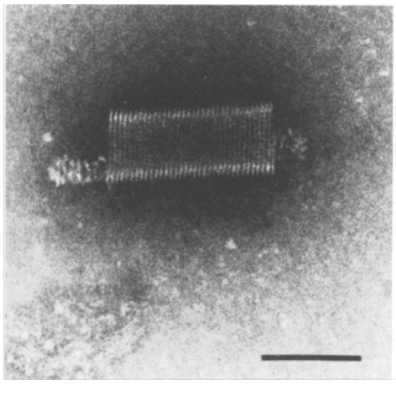

Fig. 7. A coriander feathery red-vein virus particle negatively stained with phosphotungstic acid indicating particle disruption and uncoiling of the helical structure. Bar represents 100 nm.

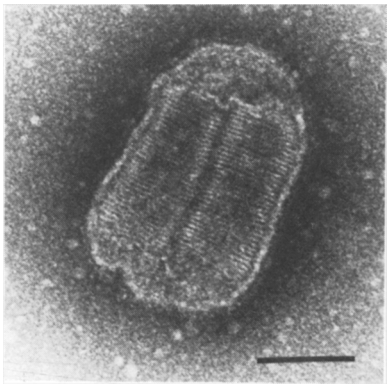

Fig. 8. A pair of coriander feathery red-vein particles negatively stained with phosphotungstic acid and enclosed in a common membrane. Bar represents 100 nm.

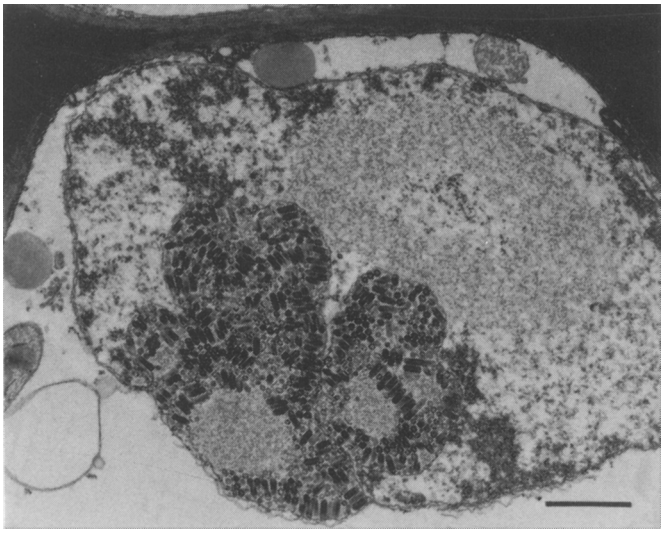

Fig. 9. Thin section of coriander, *Coriandrum sativum,* infected with coriander feathery red-vein virus, showing virions in perinuclear cisternae. Bar represents 1000 nm.

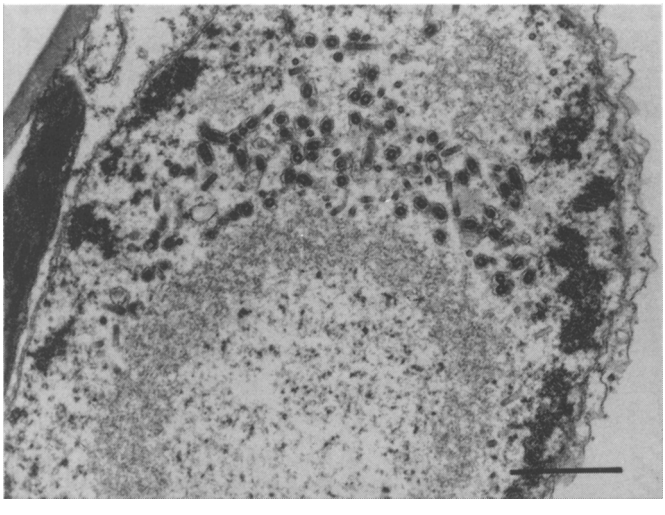

Fig. 10. Thin section of coriander, *Coriandrum sativum,* infected with coriander feathery red-vein virus, showing virions encapsulated in a nucleus. Bar represents 1000 nm.

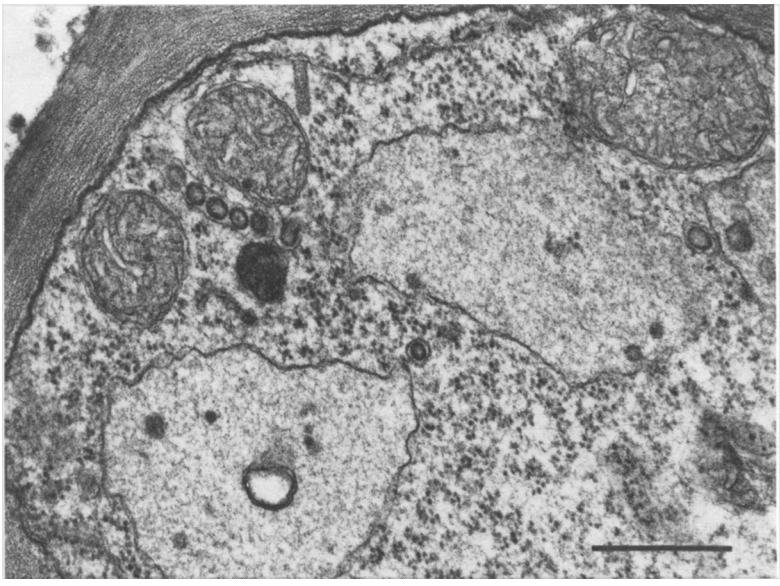

Fig. 11. Thin section of coriander, *Coriandrum sativum,* infected with coriander feathery red-vein virus, showing virions in the cytoplasm and in a tubular cisterna. Bar represents 500 nm.

Coated virus particles, in cross-section, had an electron lucent core with two dense outer rings (Fig. 12). Measurements gave a mean width and length of 74.6 ± 7.2 nm ($N = 104$) and 215.6 ± 14.5 nm ($N = 90$), respectively.

Observed variations in particle dimensions, especially in length, could have been due to differences in maturation, fixation and staining techniques, or the angle of sectioning, as well as variations in the optics of the microscope. PTA may have disruptive effects on rhabdovirus particles (MacLeod, 1968); this was evident in the present work. Virions were bacilliform in glutaraldehyde-fixed cells of infected coriander leaves, but were bullet-shaped or predominately naked helical cylinders in the PTA preparations. Negative staining with uranyl acetate may have been less disruptive to CFRVV particles than was PTA. For example, in Fig. 13 A and B, particles, though being disrupted or stripped of their protective coat, maintained a bullet-shaped structure of the nucleocapsids after UA-staining, while similar PTA preparations yielded helical nucleocapsid cylinders, mostly devoid of the rounded ends (Fig. 6 A, B) and frequently were more abundant than bullet-shaped nucleocapsids.

No rhabdovirus-like particles were seen in EM preparations (dips or sections) of non-viruliferous aphids, healthy coriander leaves or plants on which only healthy aphids had fed.

Vector range

Twelve aphid species, including *H. foeniculi,* were tested as vectors (Table 3) by allowing the insects to acquire virus by feeding. The 1 percent transmission recorded for *Myzus persicae* (Sulzer) resulted from two infections in one of three trials, using more than 500 aphids and a total of 450 test plants. *M. persicae* was an extremely incompetent vector. No attempts were made to establish the vector status of these species (other than *H. foeniculi*) by using the injection technique.

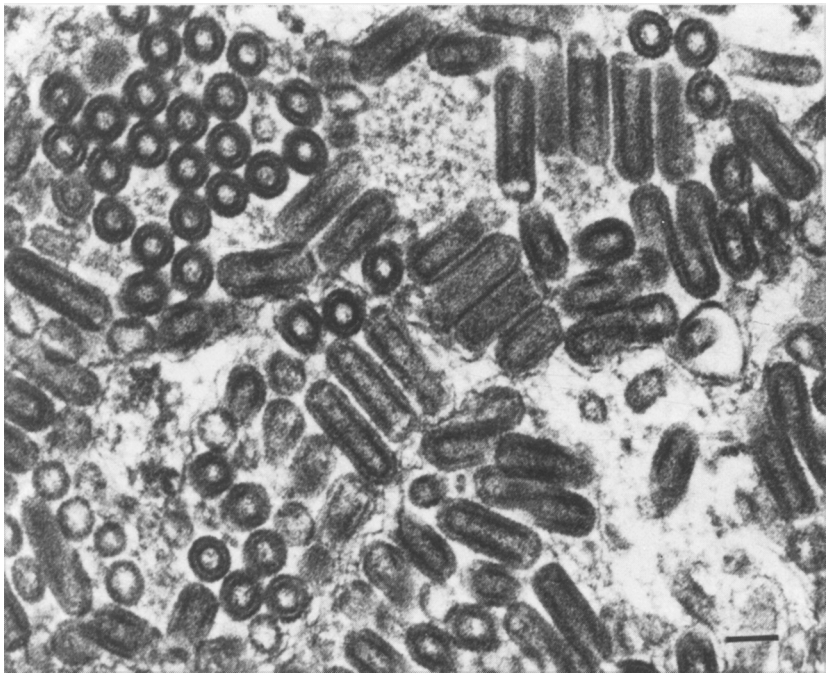

Fig. 12. Thin section of coriander leaf, *Coriandrum sativum,* infected with coriander feathery red-vein virus, showing coated particles from a perinuclear cisterna. Bar represents 100 nm.

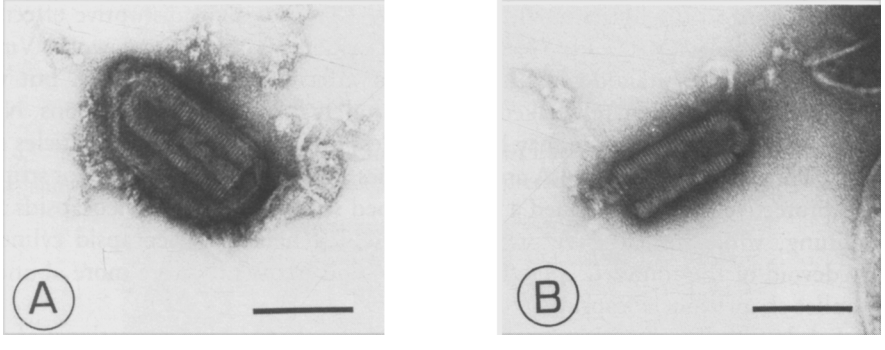

Fig. 13. (A) and (B), leaf-dip preparations of coriander, *Coriandrum sativum,* negatively stained with uranyl acetate illustrating greater preservation of virion integrity, compared with phosphotungstic acid preparations (see Fig. 6). Bars represent 100 nm.

Three of the 12 aphid species tested are commonly associated with umbelliferous plants, viz., *Aphis helianthi heracella* Davis, *A. ferruginea-striata* Essig, and *Cavariella aegopodii,* but none transmitted CFRVV in these tests. In all cases at least 10 percent of the test aphids survived until the end of the IAP.

TABLE 3.
TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS BY VARIOUS APHID SPECIES*

Species	Survival	Number of plants	
	Percent	Tested	Infected
Aphis fabae Scop	55	25	0
A. ferruginea-striata Essig	30	25	0
A. helianthi heracella Davis	90	25	0
Acyrthosiphon solani (Kaltb.)	95	150	0
Cavariella aegopodii (Scop.)	46	201	0
Chaetosiphon jacobi (HRL)	10	25	0
Hyadaphis erysimi (Kaltb.)	24	10	0
H. foeniculi (Pass.)	>95	150	120
Hyperomyus lactucae (L.)	12	25	0
Myzus ornatus Laing	53	25	0
M. persicae (Sulz.)	91	450	2
Neomyzus circumflexus (Buckt.)	90	40	0

*Lots of two or more aphids were transferred after an acquisition access period, usually of 7 days, to coriander, *Coriandrum sativum*, test seedlings for 7 to 11 days.

Field observations and laboratory tests

Honeysuckle aphids, *H. foeniculi,* were found in abundance on secondary, or summer hosts (chiefly umbelliferous plants) in the Oakland-San Francisco Bay Area. Parthenogenetic reproduction occurred on poison hemlock, cow parsnip, parsnip, and parsley. Although no quantitative data were taken, populations were observed to decline near the end of the summer months. Essig (1938) stated that many species and varieties of honeysuckle (*Lonicera* spp.) and snowberry (*Symphocarpos* spp.) served as primary or winter hosts of *H. foeniculi.* By the beginning of winter, most infestations were on primary hosts, notably honeysuckle. Colonies were found on a variety of honeysuckles in the U.C. Berkeley and Tilden Park Botanical Gardens, including California honeysuckle, *Lonicera hispidula* Torrey and Gray, var. *californica* Rehder, and southern honeysuckle, *L. sibspicata* Hooker and Arnott, var. *Johnstonii* Keck.

In April, overwintering *H. foeniculi* were randomly collected from *L. hispidula* and *L. johnstonii* in the U.C. Berkeley and Tilden Park Botanical Gardens, taken to the laboratory and transferred, in lots of two to 10 aphids, to 50 virus-free coriander plants. After an IAP of 2 to 4 days at 25 C with constant light, the aphids were moved to a second set of test plants, left for a similar IAP, then removed. None of the test plants developed symptoms of CFRVV infection, or any other disease. The evidence suggests that the sampled *L. hispidula* and *L. johnstonii* were not infected with CFRVV, and that honeysuckle may not be a host of the virus.

Incubation period of CFRVV in coriander test plants

During one phase of the experimental work involving serial transfers of aphids, records were kept of the incubation period (IP) of the virus in test plants. The IP was defined as the period in days from the beginning of the IAP until first expression of visible symptoms.

At 20 C and constant light, 125 of 390 plants were infected with a mean (range) IP of 15.8 (9 to 30) days. At 25 C, 97 of 136 plants were infected with a mean (range) IP of 15.7 (10 to 26) days. While the plants were inoculated during a 24-hour IAP at different temperatures, they were incubated under similar greenhouse conditions. The brief period at different temperatures during inoculation had no apparent effect on the IP of CFRVV in coriander. Plants inoculated early in the serial transfers, while insects were developing their full infectivity, had above average incubation periods. As the transmission sequence progressed and infectivity of the aphids maximized, the IP gradually declined (Fig. 14), only to rise again to a maximum of 26 to 30 days as the insects aged.

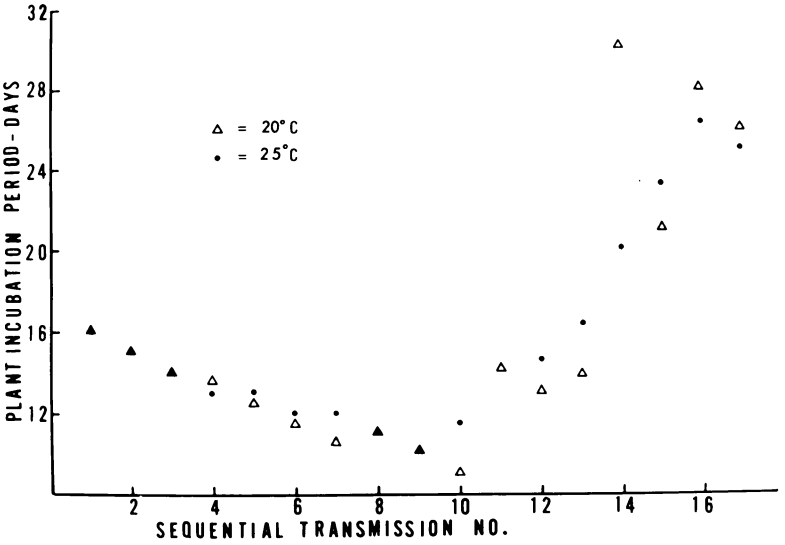

Fig. 14. Mean incubation period of coriander feathery red-vein virus in coriander, *Coriandrum sativum*, seedlings sequentially inoculated by *Hyadaphis foeniculi* aphids during serial transmission tests. Inoculations were done at 20 (△) and 25 C (●) under constant light of 8000 and 10,000 lux. The solid symbol (▲) is due to coincidence of points.

VECTOR-VIRUS RELATIONSHIPS

Acquisition

Procedure. One hundred 2-day-old larvae were caged on each of five coriander plants infected with CFRVV, and placed in a 25 C growth chamber with constant light. After 1, 2, 4, 8, 12, 16 and 32 hours, four larvae from each source were caged singly on test plants for 1 week. Surviving larvae then were moved to fresh test plants daily for 7 days. Controls were run concurrently using similar stage larvae but without access to a virus source.

Results. Acquisition occurred during a 1- to 4-hour access period to virus-source plants (Table 4). Proportions of infective insects realized after AAP of 4, 8, or 12 hours were similar, but increased with the 16- and 32-hour periods. The sample size was small and other results (Table 5) indicated acquisition could occur within 15 min at 25 C.

TABLE 4.
ACQUISITION OF CORIANDER FEATHERY RED-VEIN VIRUS BY *HYADAPHIS FOENICULI* DURING VARIABLE ACCESS TIMES ON INFECTED CORIANDER, *CORIANDRUM SATIVUM.*
Test plants were healthy coriander seedlings*

	Acquisition access period (hours)							
	0	1	2	4	8	12	16	32
Transmission	0/15	0/12	0/10	6/13	5/13	4/11	12/16	15/19
Percent	0	0	0	46	38	36	75	79

*The numerators above are the number of plants infected; denominators are the number tested.

TABLE 5.
FIRST TRANSMISSIONS OF CORIANDER FEATHERY RED-VEIN VIRUS TO AND FROM CORIANDER, *CORIANDRUM SATIVUM,* BY INDIVIDUALLY TESTED *HYADAPHIS FOENICULI* APHIDS

Acquisition access period (hr)	Days after acquisition access period							Number of aphids transmitting	Median latent period*
	7	8	9	10	11	12	13		
0.25	0	0	2	0	0	0	0	2	—
0.50	0	0	0	0	0	0	0	0	—
1	0	0	0	0	0	1	0	1	—
2	0	0	0	3	0	2	1	6	10.4
4	0	3	1	8	0	1	1	14	9.4
8	0	6	6	12	1	2	0	27	9.0
16	1	4	12	8	2	2	0	29	9.0
32	2	7	12	14	1	3	0	39	9.0

*Based on a log-probit regression of the cumulative percentage of first transmissions by individual test aphids.

Inoculation

Procedure. Last instar larvae of *H. foeniculi* reared on four different CFRVV-infected coriander plants were collected and pooled. Individual aphids then were randomly selected, caged on 175 coriander test plants, and put in a growth chamber at 25 C and constant light for an IAP of 0, 6, 12, 24, 48, 72, or 96 hours. As each IAP was terminated and the insects were removed, they were replaced with nonviruliferous aphids in all but the 96-hour treatment. When the 96-hour period elapsed, all aphids were removed and the plants were fumigated and placed in the greenhouse. An additional control consisted of a treatment in which nonviruliferous aphids had access to test plants for the entire 96-hour period.

Replacement of viruliferous by nonviruliferous aphids, at the end of each IAP, was done to determine if any symptom development was associated with toxic or mechanical injury resulting from aphid feeding.

In a second trial, 40 *H. foeniculi* apterae were caged on each of 14 virus source plants. Seven plants were kept at 20 and 25 C and constant light, respectively. After a 36-hour larviposition period, adults were removed, and the larvae were given a further 7-day

AAP. Larvae were then collected, pooled, individually caged on test plants, and then returned to their respective temperature regime. After an 0.25-, 0.5-, 1-, 2-, 4-, 8-, 16-, or 32-hour IAP, aphids were removed, and the plants were fumigated and placed in the greenhouse for symptom development. The trial was repeated once.

In a final test, 50 apterae were caged on each of four source plants at 20 C. After 24 hours adults were removed and the larvae given a further AAP of 7 days. Larvae then were collected, pooled and caged singly on test plants, and put at 25 C. The schedule of the IAP was the same as in the previous experiments.

Results. Minimum times for successful inoculation trials were 1 hour and 15 minutes at 20 and 25 C, respectively, and the probability of inoculation increased with the length of the IAP (Table 6).

TABLE 6.
EFFECT OF VARIABLE INOCULATION ACCESS PERIODS ON TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS BY THE APHID *HYADAPHIS FOENICULI* TO *CORIANDRUM SATIVUM* TEST PLANTS*

Trial	Temperature C	Inoculation access period (hours) 0	0.25	0.5	1	2	4	6	8	12	16	24	32	48	72	96
1	25	0/25	—	—	—	—	—	4/25	—	8/25	—	15/25	—	14/24	18/22	20/25
2	20	—	0/22	0/22	0/25	0/25	1/25	—	1/25	—	1/25	—	0/25	—	—	—
	25	—	0/24	0/25	0/25	1/25	0/25	—	0/25	—	2/24	—	4/24	—	—	—
3	20	—	0/25	0/25	5/25	5/25	7/25	—	11/25	—	10/25	—	19/25	—	—	—
	25	—	0/25	4/25	6/25	9/25	11/25	—	13/25	—	16/25	—	21/25	—	—	—
4	25	—	7/60	10/40	2/40	6/40	5/40	—	18/40	—	19/40	—	40/60	—	—	—

*The numerators above are the number of plants infected; denominators are the number tested.

Latent period and retention of infectivity

Procedure. Five hundred 24-hour-old larvae were fasted for 30 minutes and then caged in lots of 100 on each of five diseased coriander plants. After 0.25, 0.5, 1, 2, 4, 8, 16, and 32 hours, 10 aphids were removed from each source plant, pooled, and then caged singly on 50 individual test plants. The AAP was at room temperature, about 21 C, but the IAP was at 25 C and constant light. After 7 days on the first set of test plants, the aphids were moved to fresh sets of test plants every 24 hours until dead.

In a second trial, 3.5 day-old larvae were allowed a 3-day AAP to CFRVV-infected plants at 25 C and constant light. Individual aphids were caged on each of 50 test seedlings and subsequently moved to fresh plants at 24-hour intervals until death. Records were kept of larviposition, virus transmission and longevity of each aphid. The experiment was repeated with aphids born within a 24-hour maternal access period to diseased plants. After a 7-day AAP, 100 individuals were caged on coriander test plants. Fifteen healthy aphids that had not had access to source plants were used as controls.

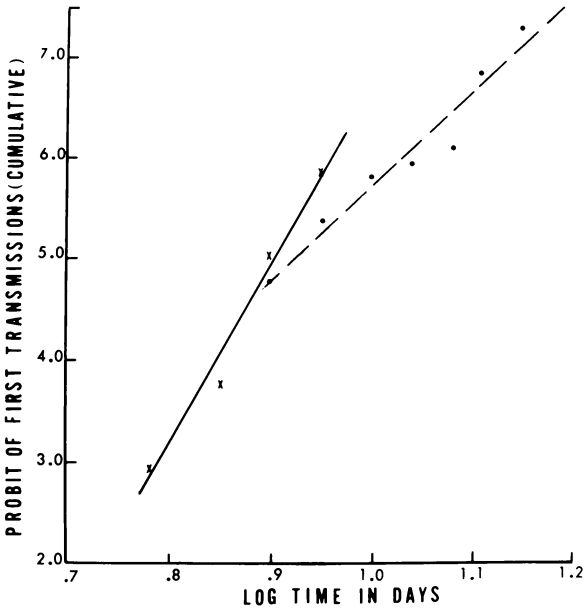

Fig. 15. Regression used to estimate the latent period of coriander feathery red-vein virus in the aphid *Hyadaphis foeniculi.* The insects were allowed an acquisition access period of 3 (———) or 7 (-------) days at 25 C and constant light of 8000 to 10,000 lux, and then transferred under similar ambient light and temperature conditions to a series of coriander, *Coriandrum sativum,* test seedlings.

TABLE 7.
LIFE TABLE AND TRANSMISSION SUMMARIZATION STATISTICS OF *HYADAPHIS FOENICULI* APTERAE TRANSMITTING CORIANDER FEATHERY RED-VEIN VIRUS FROM AND TO CORIANDER, *CORIANDRUM SATIVUM* AT 25 C AND CONSTANT LIGHT*

Statistic	Acquisition access period		
	3 days	5 days	Control†
N (number of insects tested)	50	100	15
NV (number of insects transmitting)	37	80	—
R_0 (average number of larvae per female)	34.2	21.9	22.8
T (generation time)	15.4	13.0	12.7
r_m (larvae per female per day)	0.23	0.22	0.24
V_0 (plants inoculated per female)	6.8	3.9	—
T_t (mean weighted transmission period)	19.0	10.5	—

*$R_0 = \Sigma l_x n_x$, in which l_x is the probability of the aphid being alive at age X, and n_x is the average number of larvae per female at age X; $T = \Sigma l_x n_x X / \Sigma l_x n_x$; $r_m = \log_e R_0 / T$; $V_0 = \Sigma l_x i_x$ in which i_x is the probability of transmission at age X; and $T_t = \Sigma l_x i_x X / \Sigma l_x i_x$ (based on a potential maximum transmission rate of one plant per day). The statistics were calculated for infective and the control aphids only.

†Control aphids had no access to a virus-infected plant.

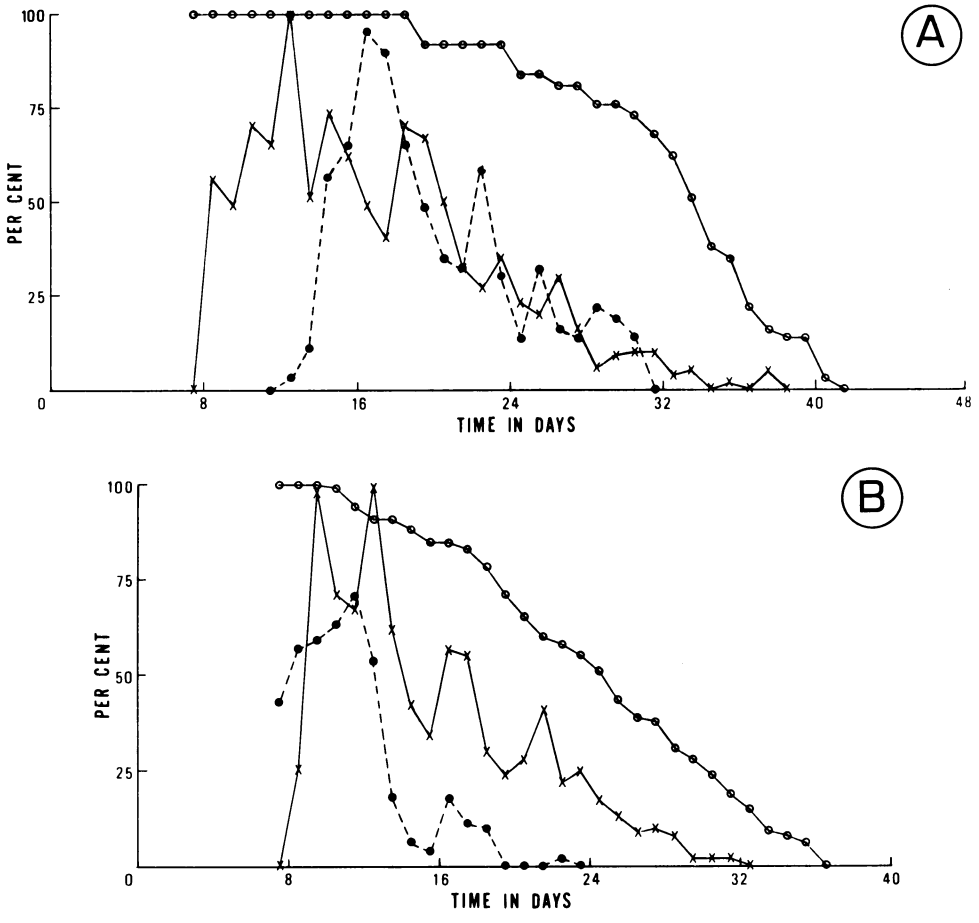

Fig. 16. Natality (X-------X), survival (O-------O) and virus transmission (●-------●) curves using *Hyadaphis foeniculi* and coriander feathery red-vein virus. Maternal apterae were given a 3-(A) or 7-(B) day acquisition access period (AAP) on infected coriander, *Coriandrum sativum*, then moved daily until death to a sequence of test seedlings. The ambient conditions were 25 C and constant light of 8000 to 10,000 lux. Natality is plotted as a percentage of maximum mean age-specific reproductive rates, estimated to be 3.3 and 2.9 larvae/female/day for the 3-day and 7-day AAP, respectively.

Results. Acquisition of CFRVV occurred in the minimum AAP of 15 minutes. The median latent period (LP_{50}) decreased as the duration of the AAP increased (Table 5).

In the second experiment, the LP_{50}, after an AAP of 3 or 7 days at 25 C, was 8.04 and 8.41 days, respectively (Fig. 15).

Table 7 summarizes the life table and transmission statistics of *H. foeniculi* after 3-and 7-day AAP on CFRVV-infected plants; Figure 16, A, B, details survival, larviposition and transmission curves for all aphids tested.

Seventy-four and 80 percent of the aphids transmitted after a 3- and 7-day AAP, respectively. Aphids given a 3-day AAP, in comparison with those given a 7-day AAP, tended to inoculate more plants, have a longer mean weighted transmission period, produce more larvae, and have a somewhat longer generation time.

Viruliferous *H. foeniculi* having a 3-day AAP survived for 12 to 35 days (mean = 26.19 days) after leaving the virus-source plants, while those given a 7-day AAP survived for 3 to 30 days (mean = 12.3 days). The period between the last transmission and the death of the viruliferous aphids varied from one to 20, with a mean of 8 days.

Healthy control aphids, with an average of 22.8 larvae per female, had a generation time of 12.8 days, and an intrinsic rate of increase of 0.24. There was little measurable effect of CFRVV on the survival or reproductive capacity of *H. foeniculi* at 25 C. Transmission efficiency declined as the insects aged. This could have been due to age-specific changes in feeding behavior, a decline in the rate of virus multiplication and translocation, or a viral-induced pathology that reduced the ability to transmit. Such a pathology, however, was not reflected by life-table statistics.

Transmission following injection

Procedure. Ninety-six adults and 23 larvae were injected at room temperature (about 21 C), with inoculum prepared from two heads of viruliferous *H. foeniculi.* Injected aphids were transferred to test plants in lots of five for an initial 48-hour IAP, and then placed singly on test plants and moved at 24-hour intervals to fresh plants until death.

Results. Thirty-four and 67 percent of the surviving adults and larvae transmitted after a LP_{50} of about 7.2 and 5.3 days, respectively (Table 8).

There was no significant evidence that larvae and adults differed in their ability to survive injection (adj. $\chi^2 = 0.15$, df 1, $p < 0.70$) or in their susceptibility to infection following inoculation (adj. $\chi^2 = 2.89$, df 1, $p > 0.05$). The average longevity of transmitters was longer than that of the non-transmitters for both adults and larvae (Table 8), but death before completion of the latent period biased the results in favor of transmitters.

TABLE 8.
TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS TO CORIANDER, *CORIANDRUM SATIVUM* BY, AND MEDIAN LATENT PERIOD IN, INJECTED *HYADAPHIS FOENICULI* *

Form	Number of aphids			LP_{50}	Average longevity	
	Injected	Surviving	Transmitting		Transmitters	Nontransmitters
				days	*days*	*days*
Adult apterae	96	44	15	7.2†	19.3	11.3
Larvae	23	12	8	5.3‡	22.3	10.8

*Aphids were injected with extracts made by triturating the head of an infected aphid in five lambda of distilled water.

†Based on a regression of a log-probit transformation using the cumulative percentage of first transmissions.

‡Estimated using Karber's equation where $LP_{50} = \frac{1}{2} \Sigma (P_{i+1} - P_i)(X_{i+1} + X_i)$, in which $i_1 = 0$, and $i_k = 1.0$.

Serial passage of CFRVV in *H. foeniculi*

Procedure. Inoculum was prepared from head extracts of aphids identified as being infected by electron microscopy or by transmission to plants. The 1st-passage donor aphids were reared on a diseased plant. The passages were initiated by injecting virus-free apterae and usually a single needle was used to inject two to five aphids. Each aphid

was transferred at 24-hour intervals to a series of seedling test plants until death. In the second and subsequent passages, inoculum was prepared from one or two infective aphids of the previous series. None of the recipients had access to an exogenous virus-infected source plant.

Results. Table 9 summarizes the results of five serial passages. Two hundred and eight of the 289 injected aphids survived beyond the minimum latent period of 5 days, and only these surviving aphids were considered in the analysis. Transmission efficiency was not consistent throughout the five passages, and in the third passage only 13 percent of the surviving aphids were inoculative.

The LP_{50} was reasonably constant, ranging from 6.0 to 7.4 days. The ability to serially pass CFRVV among successive groups of *H. foeniculi,* seemingly without a loss of titer, as evidenced by the stability of the LP_{50}, strongly suggests that the virus replicated in the host aphid.

TABLE 9.
FIRST TRANSMISSIONS TO CORIANDER, *CORIANDRUM SATIVUM,* DURING FIVE SERIAL PASSAGES OF THE CORIANDER FEATHERY RED-VEIN VIRUS IN INJECTED *HYADAPHIS FOENICULI* APHIDS*

Day since injection	First transmissions during serial passage number:				
	1	2	3	4	5
4	0	0	0	0	0
5	0	0	0	0	2
6	4	3	2	0	7
7	2	3	5	4	3
8	1	2	2	6	3
9	1	1	2	1	0
10	0	0	0	1	0
Total	8/13†	9/32	11/85	12/28	15/50
Median latent period (days)‡	6.0	6.5	6.8	7.4	6.0

*The aphids were kept at 25 C and constant light.

†The numerators are the number of insects transmitting; the denominators are the number tested and living for 5 or more days after injection.

‡Based on a regression of a log-probit transformation using the cumulative percentage of first transmissions.

Transovarial transmission

Procedure. Twenty-three 7-day-old larvae reared on virus-free coriander at 21 C and a 14:10-hour light:dark (L:D) cycle, were injected with head extracts from an infected donor reared on a diseased plant. The recipients were serially transferred in lots of five at 48-hour intervals for two transfers, and then individually moved to fresh test plants every 24 hours for 8 days. Transfers then were continued at irregular intervals.

After the injected aphids matured, larvae deposited by each aptera on each day were transferred as a lot to an individual test plant. After seven successive cohorts of larvae had had 7, 6, 5, 4, 3, 2, and 1 days of group confinement (10 days after maternal injection) respectively, survivors were individually caged on test plants for 6 days and then moved to new test plants every 48 hours. The experiment was terminated after the fourth transfer because of high mortality.

Results. Tables 10, 11, and 12 summarize the results. Eight of 12 inoculated maternal apterae that survived the injection trauma beyond 5 days transmitted, with an estimated LP_{50} of 5.31 days (Karber, 1931).

TABLE 10.
TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS TO AND FROM CORIANDER, *CORIANDRUM SATIVUM,* AT 25 C AND CONSTANT LIGHT BY INJECTED *HYADAPHIS FOENICULI* MATERNAL APTERAE SURVIVING 5 OR MORE DAYS POST-INJECTION*

	Day after injection on which transfer was made																	
Aphid	0	2	4	6	7	8	9	10	11	12	13	14	15	19	21	24	27	30
1	–	–	+	+	–	+	–	–	–	+	–	+	+	D				
2	–	–	–	–	–	–	–	–	–	–	–	–	D					
3	–	–	+	+	–	+	+	–	+	+	–	–	–	+	–	–	–	D
4	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	D
5	–	–	–	+	+	+	+	+	–	–	+	–	+	–	–	–	–	D
6	–	–	–	–	+	–	–	D										
7	–	–	–	+	–	D												
8	–	–	–	–	–	–	–	–	–	–	–	D						
9	–	–	–	D														
10	–	–	–	–	–	+	–	+	+	–	–	+	–	–	–	–	D	
11	–	–	–	–	–	D												
12	–	–	–	–	–	+	+	+	–	+	+	–	–	–	–	D		

*Plus (+), minus (–) and D symbols indicate transmission, no transmission, and aphid death, respectively. Maternal apterae were injected with a triturated head/water extract prepared from an infected aphid.

TABLE 11.
TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS TO CORIANDER, *CORIANDRUM SATIVUM,* AT 25 C AND CONSTANT LIGHT BY GROUPS OF LARVAE DEPOSITED BY INJECTED MATERNAL *HYADAPHIS FOENICULI* APTERAE

Maternal aptera	Inoculative	Test day after injection								
		2	4	6	7	8	9	10	11	12
1	yes	0*	0	7	1	2	0	1	1	2
2	no	0	0	7	1	1	4	4	(1)	3
3	yes	0	0	1	3	5	4	5	3	4
4	yes	0	0	4	2	2	1	1	4	4
5	yes	0	0	6	2	3	2	(3)	6	4
6	yes	0	0	5	1	0	0	D		
7	yes	0	0	0	2	D				
8	no	0	0	10	1	2	2	2	7	2
9	no	0	0	D						
10	yes	0	0	6	3	5	8	(2)	5	1
11	no	0	0	5	1	D				
12	yes	0	0	8	1	2	1	(2)	3	3

*Numbers, parentheses, and the symbol D, indicate the number in each group tested, one or more larvae transmitted to test plants, and death of maternal apterae, respectively.

Three of twelve lots of larvae, born 10 days after maternal injection, transmitted. In each case, the mother was inoculative (Table 11). On the 11th day, a single offspring of one "non-inoculative" maternal apterae transmitted. One-hundred and one individual

larvae were tested, beginning on the 13th day. Six transmitted, four of which were born 10 days, and two born 11 days, after the maternal inoculation (Table 12). One of the individual progeny tested remained inoculative for at least 11 days.

The data demonstrated that CFRVV could be transmitted to progeny of injected *H. foeniculi,* and that transovarial passage occurred after completion of the maternal latent period.

TABLE 12.
SURVIVAL AND TRANSMISSION OF CORIANDER FEATHERY RED-VEIN TO AND FROM CORIANDER, *CORIANDRUM SATIVUM,* AT 25 C AND CONSTANT LIGHT BY INDIVIDUAL LARVAE FROM A SEQUENCE OF COHORTS DEPOSITED BY INJECTED *HYADAPHIS FOENICULI* MATERNAL APTERAE

Time after Injection	Number of Larvae		
	Deposited	Tested*	Transmitting
days	*number*	*number*	*number*
6	59	35	0
7	17	12	0
8	22	15	0
9	21	13	0
10	20	12	4
11	30	14	2
12	23	0	—
Total	192	101	6

*Surviving aphids from each daily cohort from 12 maternal apterae were individually tested, beginning 13 days after injection.

Effects of temperature on transovarial passage

Transovarial passage following injection may have been due to accidental inoculation of embryos during injection of maternal apterae. Therefore, additional tests were made using aphids acquiring virus by feeding.

Transmission by groups of offspring

Procedure. Nonviruliferous apterae larviposited for 24 hours at 20 C and a 14:10 hour L:D cycle and then were removed. When the larvae matured, they were caged on a virus-source plant at 25 C with constant light, allowed to larviposit for 24 hours and then removed. Resulting larvae were given a 6-day AAP, after which 60 were selected, individually caged on test plants, and 30 placed in each of two growth chambers at 20 and 25 C, respectively, with constant light. The aphids subsequently were moved to fresh test plants at 24-hour intervals until death.

Each day, larvae deposited by each maternal aptera were removed and caged, as a lot, on an individual test plant for 6 days. They were then removed and the plants were fumigated and placed in the greenhouse for observation.

Early mortality (within 5 days of transfer to the first healthy test plant), and failures during the transfer process (lost or missing aphids) reduced the usable number of aphids to 26 at both 20 and 25 C.

TABLE 13.
LIFE TABLE AND TRANSMISSION SUMMARIZATION STATISTICS OF *HYADAPHIS FOENICULI* APTERAE FED ON DISEASED CORIANDER, *CORIANDRUM SATIVUM*, AND TESTED AT 20 and 25 C AND CONSTANT LIGHT*

Statistic		Temperature	
		20 C	25 C
N	(number of insects tested)	26	26
NV	(number of insects transmitting)	23	24
R_o	(average number of larvae per female)	22.8	27.1
T	(generation time)	13.7	14.3
r_m	(larvae per female per day)	0.23	0.23
V_o	(plants inoculated per female)	4.4	4.0
T_t	(mean weighted transmission period)	13.1	12.8

*$R_o = \Sigma l_x n_x$, in which l_x is the probability of the aphid being alive at age X, and n_x is the average number of larvae per female at age X; $T = \Sigma l_x n_x X / \Sigma l_x n_x$; $r_m = \log_e R_o / T$; $V_o = \Sigma l_x i_x$ in which i_x is the probability of transmission at age X; and $T_t = \Sigma l_x i_x X / \Sigma l_x i_x$ (based on a potential maximum transmission rate of one plant per day). The statistics were calculated for infective and the control aphids only.

Results. Eighty-eight and 92 percent of maternal apterae tested at 20 and 25 C transmitted (Table 13), with a corresponding maternal LP_{50} of 7.24 and 6.61 days, respectively.

The average number of plants inoculated per aphid, i.e., the net transmission rate (V_o), and the mean weighted transmission period (T_t) were slightly higher at 20 than at 25 C (Table 13).

Maximum transmission was reached by the 7th day after the initiation of the AAP in aphids tested at 25 C (Fig. 17, B) and on the 9th day for those tested at 20 C (Fig. 17, A). This difference occurred although most of the replicative cycle of the virus must have occurred during the AAP which was at 25 C for both groups.

The small sample size and random variation probably account for the intermittent secondary peaks in the rate of transmission during the later stages of the experiment (Fig. 17, A, B).

The net reproductive rate (R_o), as well as the generation time (T), of *H. foeniculi* tended to be higher at 25 than at 20 C though the intrinsic rate of increase (r_m) was similar at both temperatures (Table 13).

Table 14 summarizes the data on transovarial passage of CFRVV by maternal *H. foeniculi* apterae at two temperatures. Seventeen (65 percent) and 14 (54 percent) of the tested maternal apterae transovarially passed virus to at least one of their progeny at 20 and 25 C, respectively. One aptera at 25 C that failed to transmit virus to any plants transovarially passed virus to progeny.

A total of 575 larvae were deposited by the 23 maternal apterae tested at 20 C. Seventeen of the 23 maternal apterae transmitted and deposited 397 larvae in 272 cohorts (average = 1.46 larvae/cohort). Thirty-two (12 percent) of the cohorts transmitted virus (Table 15). At 25 C, 14 of the 24 apterae were infected. They deposited 429 larvae (61 percent of the total of 700 larvae produced) in 238 cohorts (average of 1.8 larvae/cohort), of which 20 (8 percent) contained one or more infected aphids (Table 15). Using a binomial assumption and these data, the rate of transovarial passage was estimated to be 8 percent and 5 percent at 20 and 25 C, respectively.

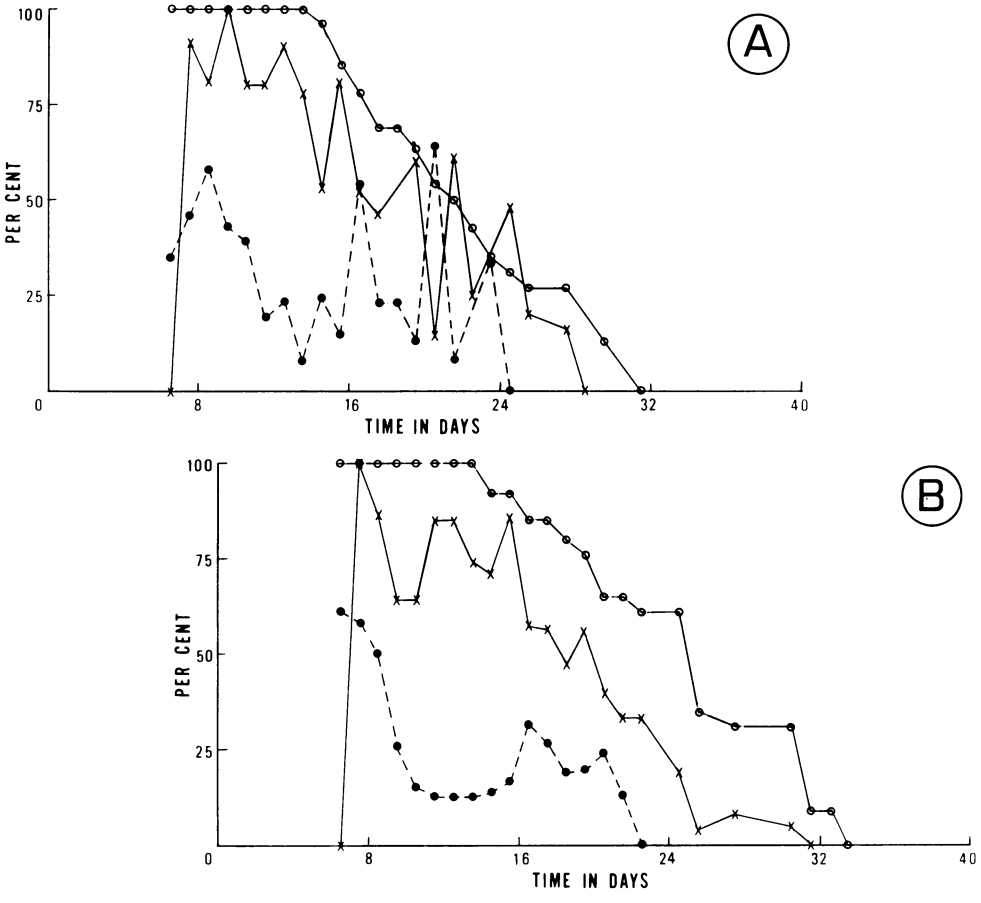

Fig. 17. Natality (X-------X), survival (O-------O) and virus transmission (●------- ●) curves comparing transmission of coriander feathery red-vein virus by *Hyadaphis foeniculi* at 20 (A) and 25 C (B) and constant light of 8000 to 10,000 lux. Larvae, born within a 24-hour maternal access period on infected coriander, *Coriandrum sativum,* plants were allowed a 6-day acquisition access period, then moved at daily intervals until death to a series of tests seedlings. Natality is plotted as a percentage of the maximum mean age-specific reproductive rate, estimated to have been approximately three larvae/female/day.

Transmission by individual offspring

Procedure. Mature apterae of *H. foeniculi* were allowed to larviposit on CFRVV source plants for 24 hours at 20 C and constant light and then removed. The larvae were given a 5-day AAP and then 10 larvae were individually caged on test plants at 20 and 25 C with constant light. These aphids (designated as maternal apterae) were moved to fresh test plants every 24 hours until death or termination of the experiment. Each larva deposited by each maternal aptera was individually caged on test plants and similarly transferred. After every transfer, the plants from which the aphids had been removed were fumigated and placed in the greenhouse for symptom observation.

Results. Table 16 summarizes the data. One maternal aptera tested at 20 C transmitted virus, and one of 39 larvae (about 3 percent) deposited by this infected maternal aptera was infective.

TABLE 14.
TRANSOVARIAL PASSAGE OF CORIANDER FEATHERY RED-VEIN VIRUS IN *HYADAPHIS FOENICULI* APTERAE AT 20 AND 25 C AND CONSTANT LIGHT. TEST PLANTS WERE CORIANDER, *CORIANDRUM SATIVUM*

Trial	Temperature C	Maternal apterae		
		Tested*	Transmitting	Transovarially passing virus
		number	*number*	*number*
1	20	26	23	17
	25	26	24	14†
2	20	10	8	1
	25	10	10	4
Total	20	36	31	18 (58%)
	25	36	34	18 (53%)

*Maternal apterae acquired virus by feeding on feathery red-vein virus infected plants. Only aphids surviving 5 or more days after completion of the acquisition access period and which were neither missing nor lost before the end of the experiment were considered to have been tested.
†One maternal aptera transovarially passed virus although she failed to transmit virus to any test plant.

All 10 maternal apterae tested at 25 C transmitted virus to test plants, and four produced infective offspring. These four apterae deposited 173 (61 percent) of the total of 285 deposited by the 10 apterae, of which 18 (10 percent) were infective. No transovarial passage occurred prior to the completion of the latent period of the virus in maternal apterae.

This experiment was discontinued when the maternal apterae were 24 days old, and therefore the rate of transovarial transmission may have been biased because of further larviposition.

Transovarial infection was inefficient, averaging 3 percent to 8 percent and 5 percent to 10 percent at 20 and 25 C, respectively. The combined results from both experiments (Table 14) gave no significant evidence that aphids tested at 20 C had a different probability of transovarially passing virus than did those tested at 25 C (18/31 vs 18/34, adj. $\chi^2 = 0.027$, df 1, $p > 0.90$).

Finally, the results from the two experiments indicated that no transovarial passage occurred earlier than 11 to 14 days after the beginning of the maternal AAP (Tables 15 and 16). This was 4 to 7 days in excess of the LP_{50} (Table 8). Most inoculative progeny transmitted virus within the first 24 to 48 hours of birth, indicating their latent periods were completed at birth or soon thereafter. Lettuce necrotic yellows virus (Boakye and Randles, 1974) and SYVV (Sylvester, 1969; Sylvester and McClain, 1978) have similar transovarial passage characteristics in the aphid *Hyperomyzus lactucae.*

Effect of aphid numbers on transmission

Rates of transmission by varying numbers of *H. foeniculi* apterae having a 10 to 12-day AAP on diseased coriander followed by a 48-hour IAP are given in Table 17.

Transmission increased with increasing numbers of aphids per test plant. However, transformation of the observed data to the expected probability of transmission by single aphids (Watson and Roberts, 1939), indicated the rate of transmission by groups was lower than expected.

TABLE 15.

TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS TO CORIANDER, *CORIANDRUM SATIVUM*, BY LARVAL COHORTS OF *HYADAPHIS FOENICULI* INFECTED TRANSOVARIALLY*

Number of infected apterae	Temperature C	Time after beginning of the acquisition access period																Frequency of pattern
		7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
17	20	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	3
		−	−	−	−	+	−	+	−	−	−	−	−	−	−	−	−	1
		−	−	−	−	+	−	+	−	−	−	−	−	−	+	−	−	1
		−	−	−	−	+	−	−	−	+	+	+	−	−	−	−	−	1
		−	−	−	−	+	−	−	−	−	−	+	−	−	+	−	−	1
		−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	+	−	+	+	+	−	−	−	−	−	1
		−	−	−	−	−	−	−	−	+	+	+	−	−	−	−	−	1
		−	−	−	−	−	−	−	−	−	+	+	−	−	−	−	−	1
		−	−	−	−	−	−	−	−	−	+	+	−	−	−	+	−	1
		−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	1
		−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	−	2
		−	−	−	−	−	−	−	−	−	−	−	−	−	−	+	−	2
14	25	−	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	−	5
		−	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	+	+	+	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	+	+	−	−	−	+	−	−	−	−	1
		−	−	−	−	−	−	+	−	+	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	−	2†
		−	−	−	−	−	−	−	−	+	−	−	−	−	−	−	−	1
		−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	1

*Maternal apterae acquired virus by feeding at 25 C and constant light, but larviposition occurred during daily transfers of maternal apterae to fresh test plants. Twenty-three and 24 apterae were tested at 20 or 25 C, respectively. A total of 575 and 700 larvae were deposited by maternal apterae at 20 and 25 C, respectively. Maternal apterae that transovarially passed virus deposited 397 and 429 larvae at the two temperatures, respectively. The minus (−) sign indicates that the larval cohort did not transmit, the (+) sign indicates that one or more larvae in the cohort transmitted.

†One maternal aptera with this pattern failed to inoculate any test plant fed upon. In this instance transmission occurred in a cohort of six larvae.

TABLE 16.

LARVIPOSITION AND TRANSMISSION RECORD OF INDIVIDUAL LARVAE DEPOSITED BY INFECTED MATERNAL *HYADAPHIS FOENICULI* APTERAE, OUT OF 10 TESTED AT EACH TEMPERATURE, THAT TRANSOVARIALLY PASSED THE CORIANDER FEATHERY RED-VEIN VIRUS*

Temperature C	Maternal aptera number	Time in days since end of acquisition access period															Total
		5	6	7	8	9	10	11	12	13	14	15	17	18	20	23	
20	1	0/0	0/0	0/0	0/2	0/2	0/6	0/1	0/3	0/2	1/5	0/1	0/4	0/0	0/9	0/4	1/39
25	1	0/0	0/0	0/0	0/4	0/4	0/4	0/5	0/1	1/3	1/4	1/4	0/9	0/2	0/10	0/6	3/56
	2	0/0	0/0	0/0	0/5	0/3	0/5	0/3	0/3	1/3	2/5	1/2	0/0	0/0	0/0D	—	4/29
	3	0/0	0/0	0/0	0/7	0/5	0/3	1/4	0/0	2/3	2/3	1/3	0/4	0/0	0/1D	—	6/33
	4	0/0	0/0	0/0	0/4	0/3	0/5	2/2	0/5	0/3	1/4	2/4	0/6	0/6	0/8	0/5	5/55
Total		0/0	0/0	0/0	0/22	0/17	0/23	3/15	0/12	4/14	7/21	5/14	0/23	0/8	0/28	0/15	19/212

*Virus acquisition occurred during a 5-day acquisition access period at 20 C and constant light on an infected coriander, *Coriandrum sativum*, plant. Following acquisition 10 apterae were moved to a series of test plants at 20 and 25 C. The numerators above are the number of larvae transmitting and the denominators are the number deposited. Symbol D indicates death of maternal aptera.

TABLE 17.

TRANSMISSION OF CORIANDER FEATHERY RED-VEIN VIRUS FROM AND TO CORIANDER, *CORIANDRUM SATIVUM*, BY VARYING NUMBERS OF *HYADAPHIS FOENICULI**

	Number of aphids per test plant							
Trial	**1**	**2**	**4**	**5**	**8**	**10**	**16**	**20**
	Ratio of plants infected to plants tested							
1	4/25	5/25	—	12/25	—	13/25		12/25
	Expected probability of transmission by single insects†							
	0.16	0.15	—	0.12	—	0.08	—	0.05
	Ratio of plants infected to plants tested							
2	7/25	4/15	12/25	—	14/25	—	19/25	—
	Expected probability of transmission by single insects							
	0.28	0.24	0.18	—	0.12	—	0.06	—

*The aphids were reared on a virus-infected plant using a 48-hr inoculation access period at 25 C and constant light.

†Estimated using a binomial assumption of equal probability of inoculation among insects, and inoculations were separate and independent events. The expected probability = $1 - q$, and the probability of transmission by n aphids = $1 - q^n$.

Virus and site of maturation	Geographical distribution	Vector	Vector relationships*			Juice inoculable	Particle size (nm)†	References
			LP	Prop	TOP			
Broccoli necrotic yellows—(cytoplasm)	England Australia	*Brevicoryne brassicae*	—	—	—	Yes	64 × 297	Hills & Campbell, 1968; Tomlinson, Webb, & Faithfull, 1972; Lin & Campbell, 1972; Garrett & O'Loughlin, 1977.
Carrot latent—(cytoplasm, perinuclear)	Japan	*Semiaphis heraclei*	9–12	—	—	No	70 to 75 × 220 to 240	Ohki, Doi, & Yora, 1978.
Coriander feathery red-vein—(perinuclear, cytoplasm, rarely)	U.S.	*Hyadaphis foeniculi* *Myzus persicae*	6–8	Yes	Yes	Yes	75 to 78 × 215 to 227	Misari, 1979.
Lucerne enation mosaic—(nucleus)	Europe	*Aphis craccivora*	—	—	—	No	85 × 250	Alliot, Giannotti, & Signoret, 1972; Leclant, Alliot & Signoret, 1973.
Lettuce necrotic yellows—(nucleus and cytoplasm)	Australia, New Zealand, England	*Hyperomyzus lactucae* *H. carduellinus*	5–18	Yes	Yes	Yes	66 × 227	Stubbs & Grogan, 1963; Harrison & Crowley, 1965; O'Loughlin & Chambers, 1967; Randles & Carver, 1971; Boakye & Randles, 1974.
Parsley latent (unknown)	England	*Cavariella aegopodii*(?)‡	—	—	—	Yes	87 × 214	Tomlinson & Webb, 1974; Martelli & Russo, 1977.
Raspberry vein chlorosis—(cytoplasm)	Canada, Europe, USSR, New Zealand	*Aphis idaei*	—	—	—	No	65–80 × 430–500	Cadman, 1952; Jones, Murant & Stace-Smith, 1977; Stace-Smith & Lo, 1973.

Sonchus yellow net—(nucleus)	U.S.	*Aphis coreopsidis*	—	—	—	Yes	94 × 248	Christie, Christie & Edwardson, 1974; Jackson & Christie, 1977.
Sowthistle yellow vein—(cytoplasm, perinuclear)	U.S., England, Europe	*Hyperomyzus lactucae* *Macrosiphum euphoribae*	8	Yes	Yes	No	80 × 220	Duffus, 1963; Richardson & Sylvester, 1968; Duffus & Russell, 1969; Sylvester & Richardson, 1969; Peters, 1971; Ozel, 1971, 1973; Behncken, 1973; Schultz & Peters, 1976.
Strawberry crinkle—(cytoplasm)	Worldwide	*Chaetosiphon fragaefolii* *C. jacobi* *Aphis forbesi*(?)§	6	Yes	—	No	69 × 190 to 380	Zeller & Vaughan, 1932; Prentice & Woollcombe, 1951; Frazier, 1968; Frazier & Mellor, 1970; Richardson, Frazier & Sylvester, 1972; Babovic, 1976.

*LP = latent period in days, Prop. = propagative, or multiplying in the vector, TOP = transovarial or vertical transmission.

†Sizes for BNYV, LNYV, PLV, SYNV, are based on negatively-stained leaf-dip or purified preparations, while those for CLV, CFRVV, SYVV, and SCV, are based on thin-sections of plant material.

‡Tomlinson and Webb (1974) illustrated particles of a rhabdovirus obtained from parsley by mechanical inoculation. Martelli and Russo (1977), on the basis of personal communication with Tomlinson, listed it as being aphid-transmitted, and finally, Francki, Kitajima, and Peters (1981) gave the vector as *Cavariella aegopodii*, without reference as to where they obtained their information. Since this species apparently was the only one used by Tomlinson and Webb, we assume the aphid transmission was with *C. aegopodii*.

§Unconfirmed report by Babovic (1976).

DISCUSSION

Coriander feathery red-vein virus is considered to be a propagative aphid-borne rhabdovirus. Evidence for this conclusion includes:

(1) Visualization of rhabdoviruslike particles in negatively-stained preparations from infected plants as well as from infective aphids, and in thin sections of infected plants.
(2) A prolonged dosage and temperature sensitive latent period.
(3) Maintenance of titer (as evidenced by the duration of the latent period) through five serial passages among virus-free *H. foeniculi.*
(4) Transovarial passage of the virus by apterous viviparae.

At least 62 viruses in the family Rhabdoviridae are listed as animal or plant pathogens (Knudson 1973), and they have been the subject of a series of recent reviews (Howatson, 1970; Hummeler, 1971; Peters, 1971; Francki, 1973; Knudson, 1973; Wagner, 1975; Martelli and Russo, 1977; Francki, Kitajima, and Peters, 1981).

Table 18 gives data on aphid-transmitted rhabdoviruses, and some of their characteristics. Three, in addition to CFRVV, infect umbelliferous plants, viz., parsley latent virus (PLV) associated with the carrot motley dwarf complex of parsley in England (Tomlinson and Webb, 1974), cow-parsnip mosaic (CPMV) (Polák, 1966; Polák, Králík, and Limberk, 1977), and carrot latent virus (CLV) from Japan (Ohki, Doi, and Yora, 1978).

PLV is mechanically transmissible to *Nicotiana clevelandii* and vectored by the yellow willow aphid, *Cavariella aegopodii* Scop. (Tomlinson and Webb, 1974; Martelli and Russo, 1977). CPMV also is sap transmissible to parsley, but no vectors are reported (Polák, Králík, and Limberk, 1977), and CLV is not juice inoculable, but is aphid transmitted, by *Semiaphis heraclei* (Ohki, Doi, and Yora, 1978). CFRVV resembles CLV in that it is symptomless in many unbelliferous hosts. Unlike CLV, however, it is juice inoculable and also causes distinct and persistent symptoms in celery.

Electron microscopic studies indicate CFRVV has, *in situ,* a particle morphology similar to other aphid-borne rhabdoviruses, viz., lettuce necrotic yellows (LNYV) (O'Loughlin and Chambers, 1967), sowthistle yellow vein virus (SYVV) (Richardson and Sylvester, 1968), strawberry crinkle virus (SCV) (Richardson, Frazier, and Sylvester, 1972), and *Sonchus* yellow net virus (SYNV) (Christie, Christie, and Edwardson, 1974) as well as those infecting Umbelliferae which, *in situ,* are bacilliform with particle dimensions of 87 × 214 nm, 90 × 265 nm, and 70 to 75 × 220 to 240 nm, for PLV, CPMV, and CLV, respectively (Tomlinson and Webb, 1974; Polák, Králík, and Limberk, 1977; Ohki, Doi, and Yora, 1978). With dimensions of 75 × 215 nm, CFRVV most nearly resembled CLV in size.

Leaf- and head-dip preparations of CFRVV are like CLV in the frequent occurrence of uncoated fragments of transversely-striated, helically-wound nucleocapsid cylinders (Ohki, Doi, and Yora, 1978) rather than the coated bullet-shaped or bacilliform particles often found with other rhabdoviruses.

Tests showed parsnip, from which CFRVV was originally recovered, to be a symptomless host. This may explain why CFRVV has not been previously noticed by plant pathologists or vector-entomologists. The aphid vector is ubiquitous and cosmopolitan (Hottes and Frison, 1931; Eastop and Hille Ris Lambers, 1976), and CFRVV shows definite symptoms in celery, suggesting it does not commonly infect celery in the field.

Symptoms resemble celery yellow spot (CYSV), described by Freitag and Severin (1945). They found naturally infected parsnip showed a mild mosaic when infected with CYSV, but poison hemlock was a symptomless carrier. The virus was not juice inoculable,

and was transmitted specifically by *H. foeniculi* to celery from both parsnip and poison hemlock. The yellow-spot symptom syndrome was produced in celery. Infectivity was retained by aphids for 12 days in trials where groups were given 23 daily transfers. Hollings (1964), on the basis of symptoms, tentatively identified a disease of celery found in several areas of England as CYSV. Symptoms occurred following mechanical inoculation of celery using juice from a celery plant infected with both cucumber mosaic virus (CMV) and CYSV. Passage through *N. glutinosa* apparently eliminated CYSV. Additional tests suggested mechanical transmission of CYSV occurred only when CMV was present. CFRVV differs from the virus(es?) in both reports in that it is juice inoculable to *N. glutinosa* in the absence of any apparent mixed infection, and is symptomless in parsnip.

Of 24 species of plants in eight families tested, only *N. clevelandii, N. gultinosa,* and their hybrid were susceptible to CFRVV by sap-inoculation, and convincingly so only when using inoculum derived from aphid-infected *N. clevelandii* or *N. glutinosa.* In this property, CFRVV resembles PLV (Tomlinson and Webb, 1974).

Twelve species of aphids, including *C. aegopodii,* were tested for their ability to transmit CFRVV, but only *H. foeniculi* was a competent vector. *Myzus persicae* gave 1 percent transmission in one of three tests. CYSV was not transmitted by *M. persicae,* nor *C. aegopodii.* In this it differes from CFRVV and from PLV. PLV is transmitted by *C. aegopodii,* and CLV by *Semiaphis heraclei.* Apparently *H. foeniculi* was not used in tests with either of these viruses (Martelli and Russo, 1977; Ohki, Doi, and Yora, 1978). *S. heraclei* does not occur in the U.S.

The results obtained in this work generally conform to established patterns of vector-virus relationships for aphid-borne rhabdoviruses. Acquisition and inoculation access minima, in the range of 15 minutes, are consistent with other reports for SYVV (Duffus, 1963) and LNYV (Boakye and Randles, 1974). CFRVV has a prolonged, dosage sensitive, latent period in the aphid vector as does SYVV (Duffus, 1963; Sylvester, Richardson, and Behncken, 1970). Transmission during early phases of the latent period, and in later stages during the retention period, resulted in longer plant-incubation periods. This agrees with reports on SYVV (Duffus, 1963) and SCV (Frazier, 1968), and has been interpreted as a dosage response and as evidence of multiplication in the aphid vectors (Duffus, 1963).

Serial passage, with a stable latent period, suggests maintenance of titer, and multiplication. Again this is consistent with reports on SYVV (Sylvester and Richardson, 1969) and SCV (Sylvester, Richardson, and Frazier, 1974).

A consistent, but low rate of transovarial passage is similar to that found with LNYV (Boakye and Randles, 1974) and SYVV (Sylvester, 1969; Sylvester and McClain, 1978).

Reasons for transmission by groups of vectors to be less than expected under an assumption of equal probability of inoculation and separate and independent inoculation events has been discussed by various authors (Smith and Lea, 1946; Gibbs and Gower, 1960; Bindra and Sylvester, 1961; Caudwell, 1977). The possible presence of resistant or immune plants in test populations of coriander should be investigated.

Until more rigorous tests are developed to test for relationships among aphid-borne rhabdoviruses infecting Umbelliferae, the host range, symptomatology, vector specificity, mechanical inoculability, size, and PTA-fragility of CFRVV, suggest it would be prudent at present to regard this virus as a distinct, previously undescribed entity.

SUMMARY

Honeysuckle aphids, *Hyadaphis foeniculi* (Passerini), collected on symptomless parsnip (*Pastinaca sativa* L.) transmitted a virus that induced a red vein-banding symptom in coriander (*Coriandrum sativum* L.). Symptoms were distinguishable from a normal leaf-reddening that developed in coriander grown under high light intensity. The virus is believed to be undescribed and the name coriander feathery red-vein virus (CFRVV) is proposed.

Negatively-stained diseased leaf- and infective aphid head-dip preparations examined by electron microscopy had bullet-shaped particles and uncoated fragments of nucleocapsids with prominent transverse helical striations. The latter were more frequent in dip preparations than were bullet-shaped particles. Thin sections of plant material revealed bacilliform particles about 74 nm wide and 216 nm long. They usually were found partially or completely enclosed by the inner membrane of the nuclear envelope or aligned in invaginated nuclear cisternae. Isolated uncoated and membrane-bound particles were less frequent in cytoplasm. In cross-section, coated virions had an electron lucent core surrounded by two electron-dense outer rings.

Mechanical transmission was not successful from infected coriander to any host tested, with the possible exception of *Nicotiana clevelandii* Gray. However, using aphid-inoculated *N. clevelandii,* or *N. glutinosa* L. as sources, mechanical transmission, evidenced by development of systemic symptoms, was obtained to both of these species as well as to *N. clevelandii* x *glutinosa* hybrids. No evidence was obtained for seed or dodder (*Cuscuta campestris* Yunck.) transmission.

A limited host range study using aphid-inoculation of 18 species in five plant families indicated that some species in the Solanaceae and Umbelliferae were susceptible. Symptoms occurred only on coriander, celery (*Apium graveolens* L.), *N. clevelandii, N. glutinosa* and their hybrid. Five umbelliferous species, viz. chervil (*Anthriscus sylvestris* L.), water hemlock (*Cicuta* sp.), carrot (*Daucus carota* L.), fennel (*Foeniculum vulgare* Mill.), and parsley (*Petroselinum crispum* Nym.), were found to be symptomless hosts of the virus.

Twelve species of aphids were tested, but with the exception of an occasional transmission by *Myzus persicae* (Sulzer), *H. foeniculi* was the only consistent vector.

Hyadaphis foeniculi could acquire virus from infected coriander in a 1- to 4-hour acquisition access period (AAP). After a median latent period (LP_{50}) of 8.5 days at 25 C and constant light, aphids could transmit CFRVV within a 15- to 30-minute inoculation access period (IAP). The LP_{50} was temperature and dosage sensitive, tending to decrease with increasing duration of the AAP. The mean weighted period of transmission ranged from 12.8 to 19.5 days.

The plant incubation period was independent of temperature (20 or 25 C) during inoculation, and ranged from 9 to 30 days with a mean of about 16 days. It averaged approximately 16 days when inoculation occurred in the early phases of the prolonged infectivity period of the vectors, then declined to a minimum of about 10 days, but again gradually increased to a maximum of some 30 days as vectors aged.

The virus was transmissible to *H. foeniculi* by needle inoculation. Larvae survived injection less well than adults, but were more efficient transmitters with a shorter LP_{50}.

Transovarial passage occurred, with nearly 55 percent of inoculative maternal viviparae producing one or more infective larvae. The rate of transovarial passage, based on the total number of larvae produced, varied from 3 to 10 percent. Transovarial passage did not occur earlier than 10 to 14 days after maternal virus acquisition, whether this was by

needle inoculation or by feeding on infected plants. The latent period in larvae transovarially infected usually was completed at birth.

The reproductive rate and generation time of noninoculative *H. foeniculi* was 22.8 and 12.8 days, respectively at 25 C and constant light, with an intrinsic rate of increase of 0.24. The corresponding values for inoculative insects were 27.9, 14.8, and 0.22, respectively. There was no evidence that viral infection affected longevity or the reproduction of the aphids.

Virus was passed serially to five successive groups of aphids, using needle inoculation. The LP_{50} was similar in each passage, having a mean (range) of 6.5 (6.0 to 7.2) days.

The rate of transmission by groups of insects was less than expected, assuming each aphid had a similar probability of transmitting and each inoculation was a separate and independent event.

CFRVV appears to be distinct from other plant rhabdoviruses reported to infect umbelliferous plants and is considered to be a previously undescribed propagative, aphid-transmitted, plant rhabdovirus.

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