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Laboratory Detection of Viruses and Mycoplasmalike Organisms in Strawberry

The cultivated strawberry (*Fragaria* × *ananassa* Duchesne), an important fresh market and processed fruit crop in many parts of the world, is infected by many viruses and mycoplasmalike organisms (MLOs). Currently, 29 are known, and we can anticipate that more will be found. A few of these pathogens kill infected strawberry plants, but the majority reduce productivity while inducing no distinctive symptoms. Because vegetatively propagated cultivars are used to grow this crop, techniques other than diagnosis by visual symptoms have been necessary to determine the virus status of potential strawberry planting material. Leaf graft bioassays are currently used to detect most viruses in strawberry plants (6). Recent developments in plant virus serology and molecular biology have provided rapid, accurate, and sensitive techniques to augment or replace these standard bioassays.

The USDA's Agricultural Handbook 631 (6) provides a convenient review of the literature pertinent to strawberry viruses and MLOs and their laboratory detection through 1980. Our purpose in this article is to present developments in this field that have been reported in the literature over the last 8 years.

Aphid-borne Diseases

Strawberry mottle virus (SMV). In 1968, Frazier (10) mechanically transmitted this semipersistent aphid-borne virus to *Chenopodium quinoa* Willd. to produce characteristic mild vein banding, vein necrosis, and epinasty (Fig. 1). This work was recently repeated (2,14). From both *C. quinoa* and *F. vesca* L. VS-1 infected with SMV, two bands of double-stranded RNA (dsRNA) were detected with relative molecular weights of approximately 5.4 and 4.6 million daltons (2). In other experiments (16), however, no dsRNA bands could be detected in *F. vesca* infected with SMV by aphid inoculations.

The virus was successfully transmitted mechanically or by the aphid *Chaetosiphon fragaefolii* (Cockerell) from *C. quinoa* to *F. v.* var. *semperflorens* cv. Alpine, where it produced symptoms typical of strawberry mottle disease (14). This contrasts with unsuccessful attempts by others either to return the virus from *C. quinoa* and other herbaceous hosts to *F. vesca* by means of aphids, grafting, and dodder (2,10) or to purify the virus (2). These discrepancies may reflect differences among isolates of SMV. Partial purification of SMV from infected *C. quinoa* leaves by means of homogenization in buffer, polyethylene glycol precipitation, low- and high-speed centrifugation, and CsCl equilibrium density gradient centrifugation gave rise to preparations containing isometric viruslike particles having a buoyant density of 1.35/cm^3, with a particle diameter of 30 nm, as determined by electron microscopy of preparations stained with 2% neutral phosphotungstate. Such particles were absent from uninoculated control plants (14).

Strawberry vein banding virus (SVBV). SVBV (Fig. 2) was previously characterized sufficiently to establish its group status as a plant caulimovirus (23),

Cooperative research between the United States Department of Agriculture, Agricultural Research Service, and the Oregon Agricultural Experiment Station. Technical paper 8496 of the latter.

although the nature of the viral genome was not confirmed. The SVBV genome has since been cloned and characterized as a 7.8-Kb circular, double-stranded DNA with features typical of the caulimovirus group. Full-length clones of the viral genome have proved useful as sensitive and specific probes in dot hybridization tests for the detection of the virus in infected strawberry plants (30).

Strawberry crinkle virus (SCV). This rhabdovirus (Fig. 3), vectored persistently by *C. fragaefolii*, is successfully transmitted from *F. vesca* cv. UC-4 to UC-4 by petiole insert leaflet grafting with symptom-bearing leaflets throughout the year. Transmissions failed with symptomless leaflets from infected plants, and the percentage of successful transmission was lowest when grafts were made during the winter months. Electron microscopic evaluation of SCV-infected leaf tissues at intervals after grafting revealed that maximum titers of viruslike particles (VLP) occurred about 1 week after appearance of the first symptoms. There appears to be extreme variability in VLP titers among samples from symptom-bearing plants, even when harvested at the time of maximum VLP production (7). Similar studies of SCV in West Germany indicate that infected *F. vesca* cv. UC-5 leaves contain typical rhabdoviruslike particles in cytoplasmic vesicles (15).

By use of 50-g samples of leaves from infected UC-4 and of standard extraction procedures, dsRNA bands were associated with SCV infection. The bands had relative molecular weights of 4.2, 2.3, and 2.1 million daltons. No dsRNA bands were detected in comparable, ungrafted UC-4 samples. The procedure may be useful for tentative identification of suspected SCV isolates, but the method is too insensitive and slow to be valuable for determining that SCV is absent in a test sample (13). More important, because the presence of dsRNA species is atypical of rhabdoviruses, these results could also be interpreted as indication of as yet unidentified viruses that may be associated with the strawberry plants tested.

After injection with extracts from viruliferous aphids (*Chaetosiphon jacobi* Hille Ris Lambers), the polyphagous aphid *Myzus ornatus* (Laing), which does not normally transmit SCV, was able to transmit SCV to *F. vesca* plants at a low frequency, giving rise to typical symptoms of strawberry crinkle disease (31). Similar studies with another non-SCV vector, the polyphagous aphid *Macrosiphum euphorbiae* (Thomas), showed that injected aphids could infect *F. vesca* cv. Alpine, *Nicotiana glutinosa* L., and *N. clevelandii* Gray. Infected *Nicotiana* plants showed mosaic, vein clearing, epinasty, stunting, and chlorotic lesions that turned necrotic. *M. euphorbiae* was able to transmit SCV from *Nicotiana* plants back to Alpine plants, from which typical rhabdovirus particles were identified by electron microscopy (32). These expanded host range studies have permitted the identification of alternate hosts, including *Physalis* species, that can be mechanically inoculated and in which the virus replicates to higher titers. The detection of the virus in such plants has been possible from as little as 1 g of tissue with biotinylated lectins as probes in an immunoblot type of analysis, essentially as described by Adam et al (1). The method has proved useful in identifying the best source of plant tissue for virus production and in developing an optimal purification protocol (T. J. Morris, *unpublished*).

Strawberry mild yellow-edge virus (SMYEV). SMYEV (Fig. 4), persistently transmitted by *C. fragaefolii*, was found to be serologically related to the luteovirus beet western yellows virus (BWYV) by means of immunospecific electron microscopy (ISEM). Although BWYV antiserum trapped partially purified preparations of SMYEV, there was no subsequent decoration in ISEM of SMYEV particles by BWYV. Therefore, although SMYEV can be regarded as a luteovirus, its serological relationship to BWYV is not close (26).

In 1984, Yoshikawa et al (36) published the first report on studies of SMYEV ultrastructure in infected cultivated strawberry and *F. vesca* cultivars UC-5 and UC-6. They found isometric 22- to 25-nm VLP only in phloem parenchyma, sieve tubes, and companion cells of SMYEV-infected plants. These VLP occurred in aggregated masses in cell cytoplasm, nuclei, and vacuoles. The cytoplasm of these cells became vesiculate, with nucleic-acid-like fibrils interspersed with VLP replacing the organelles and cytoplasm. Such cells became necrotic. In the United States, a developmental study of SMYEV ultrastructure in infected *F. vesca* cv. UC-4 was undertaken by Florance et al (8). Four weeks after its transmission to *F. vesca* by *C. fragaefolii*, SMYEV was first detected by electron microscopy in phloem parenchyma cells of the youngest leaves and occurred sometimes in aggregates of 30-nm-diameter VLP.

Purification of dsRNA from SMYEV-

Fig. 1. Chronic symptoms of strawberry mottle virus on *Fragaria vesca* var. *semperflorens* cv. Alpine. (Right) Severe and (left) moderate strains. (Courtesy USDA-ARS)

Fig. 2. Symptoms of strawberry vein banding virus on *Fragaria vesca* var. *semperflorens* cv. Alpine.

Fig. 3. Symptoms of strawberry crinkle virus on *Fragaria vesca* var. *semperflorens* cv. Alpine.

Fig. 4. Symptoms of strawberry mild yellow-edge virus on *Fragaria vesca* cv. UC-4. (Courtesy USDA-ARS)

infected strawberry cultivars revealed three distinct bands at relative molecular weights of 3.8, 2.8, and 1.3 million daltons. At least 20 g of fresh strawberry leaf tissue was required in their preparation. These dsRNA bands for SMYEV resemble those found for the well-characterized luteoviruses barley yellow dwarf virus and BWYV. In addition, relatively low molecular weight bands at 0.9 and 0.5 million daltons were routinely found in uninoculated plants of the two strawberry cultivars used for this work in clones that indexed negative for SMYEV by standard leaflet graft indexing to *F. vesca* indicators (25). cDNA clones were obtained from SMYEV dsRNA templates purified from *Rubus rosaefolius* Smith and were successfully used to detect SMYEV in infected strawberry and *R. rosaefolius* tissues (22).

Clones of several U.S. Pacific Northwest strawberry cultivars that tested free from known viruses by leaf graft analysis on standard strawberry virus indicator plants were used as sources for virus purification following previously published methods for SMYEV (6,21). Isometric (28-nm) VLP were found in some of these cultivars (e.g., Benton) that cosedimented with VLP previously associated with SMYEV infection. The identity of the VLP in graft-negative Benton is not yet determined (20).

Strawberry latent C virus (SLCV). SLCV (Fig. 5), a persistent, aphid-borne virus, had been reported from only the eastern United States (6) until it was found in two strawberry cultivars in Japan (35). Leaflet grafts from two Japanese isolates of SLCV induced symptoms typical of SLCV on the *F. vesca* indicator UC-4 but not on UC-5, which is reported (11) in the United States to be insensitive to this virus. Electron microscope studies of SCLV-infected leaf tissue sections from Japan and the United States revealed the presence of rhabdoviruslike particles 190–380 × 68 nm in cell nuclei but not in cytoplasm. Viroplasms were frequently found in both nuclei and cytoplasm of infected cells. This is the first report of the occurrence of rhabdoviruslike particles in nuclei of strawberry cells (SCV virions are found only in the cytoplasm) and provides a method other than bioassay for identifying SLCV (35).

Strawberry pseudo mild yellow-edge virus (SPMYEV). Strawberry pseudo mild yellow-edge virus (Fig. 6) is a semipersistent virus originally known from one report of its natural occurrence in the United States (9). Later it was found in Japan in the strawberry cultivar Hoko-wase, and it was readily transmitted in a semipersistent manner by the aphids *C. fragaefolii* and *Aphis gossypii* (Glover). Purification from SPMYEV-infected Alpine strawberry yielded filamentous VLP 625 (600–650) × 12 nm with a buoyant density of 1.32 g/cm^3. The virus had a single-stranded RNA with a relative molecular weight of 2.5 million daltons and a coat protein subunit with a relative molecular weight of 33,500 daltons. Parallel uninoculated Alpine plants contained no such particles, so the virions were concluded to be associated with SPMYEV infection and are referred to as SPMYEV virions. This virus is serologically related to carnation latent virus and is regarded as a new member of the carlavirus group. A dot immunobinding assay was developed for rapid detection of SPMYEV in infected strawberry leaf sap. Polyclonal rabbit antiserum against SPMYEV reacted positively with a type isolate of SPMYEV in the United States. This is the first published report of an antiserum capable of detecting an aphid-borne virus in infected strawberry plant samples from the field (34,37).

Until the present gaps in the methodology for laboratory detection of the major strawberry virus and viruslike pathogens are closed, determination of the virus status of strawberry planting material will continue to depend on leaf graft bioassays

Leafhopper-borne Diseases

Strawberry green petal disease (Fig. 7), caused by a mycoplasmalike organism (SGPMLO), is an important leafhopper-transmitted disease of strawberry. SGPMLO is characterized by small, red-leaved plants bearing abnormal fruit and frequently showing diagnostic symptoms of virescence. The same, or a related, MLO produces phyllody in ladino, red, and alsike clovers (*Trifolium* spp.) in northeastern North America and in western Europe. Polyclonal rabbit antisera have been produced against the clover phyllody MLO from graft-inoculated periwinkle (*Catharanthus roseus* (L.) G. Don). Extensive cross-absorption against healthy *C. roseus* sap yielded antisera that gave strong positive reactions in enzyme-linked immunosorbent assays (ELISA) with both phyllody-affected clover and green-petal-affected strawberry but not with healthy plants (3), thereby confirming the association between these two MLOs.

In Europe, antisera have been raised to several other MLOs graft-inoculated into periwinkle, including several aster yellows MLO (AYMLO) isolates from Europe and the United States. AYMLOs are known to infect cultivated strawberry. Although not tested directly with green-petal-affected strawberry, none of these polyclonal antisera gave any reaction with clover or periwinkle infected with SGPMLO (4). Also, there was no cross-reaction between the SGPMLO and an aster yellows-related monoclonal antibody prepared against a primula yellows MLO (M. F. Clark et al, *unpublished*). Monoclonal antibodies have been developed against a North American isolate of AYMLO (19), but these have not been evaluated for detecting AYMLO in strawberry plants.

Several other MLOs have been implicated as the etiological agents of several strawberry diseases, including lethal decline syndrome (6). Experimental transmission of the western-X MLO to strawberry produced symptoms typical of this disease (27), confirming a previous report (12). X-disease MLOs were detected in strawberry extracts using cloned DNA probes of the MLO genome (18). These reports establish the utility of dot-blot hybridization for the detection of MLO infections in strawberry plants.

Nematode-borne Diseases

In the United States, tomato ringspot virus (TmRSV) (Fig. 8) has been reported to infect cultivated strawberry in the field, where it is vectored by several species of dagger nematode (*Xiphinema* spp.) (5). This virus is readily detected in sap from infected strawberry plants by ELISA with antisera prepared against TmRSV from a number of other hosts.

In Europe, four nematode-borne viruses infect strawberries in the field: arabis mosaic virus (AMV) and strawberry latent ringspot virus (SLRV), vectored by *X. diversicaudatum* (Micoletzky) Thorne, and raspberry ringspot virus (RRV) and tomato black ring virus (TBRV), vectored by *Longidorus elongatus* (de Man) Thorne & Swanger. All four are readily identified by ELISA in infected strawberry plant sap (6).

Disease with Unknown Vector

Tobacco streak virus (TSV) (Fig. 9) has been implicated as the causal agent in the strawberry disease called necrotic shock, named after the symptoms caused in graft-inoculated *F. vesca*. TSV is

symptomless in infected strawberry cultivars, which become infected in the field by unknown means. TSV can be routinely detected by ELISA in infected strawberry plants using antisera prepared to TSV from *Rubus* (6). Recently, Stenger et al (29) compared ELISA, using homologous, polyclonal antiserum prepared against TSV from strawberry, with dot hybridization assays, using a cloned complementary DNA (cDNA) of a small portion of the viral genome. The results showed that ELISA and dot hybridization assays were equally effective at detecting TSV in symptomless, field-infected strawberry plants. The authors (29) suggested that ELISA is the preferred method for routine detection because sample preparation is simpler and radioactivity is avoided. Although this study did not attempt to optimize the sensitivity of the hybridization assays by using larger clones and different extraction protocols, it did establish for the first time the utility of hybridization assays for the detection of small RNA viruses in field-collected strawberry tissue.

A Minor Disease and a Disorder Not Transmissible by Graft

Tomato bushy stunt virus (TBSV). There is a single report from Czechoslovakia that TBSV occurs naturally without producing symptoms in cultivated strawberry (24). This virus has a wide host range, is water-transmitted, and is readily detected from infected plant sap by ELISA (33). The extent of its occurrence and its economic importance in cultivated strawberry remain to be determined.

June yellows (JY). JY (Fig. 10) is a non-graft-transmissible disorder of cultivated strawberries (6). The etiology of JY remains obscure, although it is a major concern of strawberry breeders because it appears to be transmitted to seedling progenies from parental lines known to carry JY. JY may suddenly appear in such seedlings, advanced selections, or cultivars years later, making them chlorotic, weak, and unproductive. T. J. Morris (*unpublished*) was not able to consistently detect the presence of either dsRNA or small circular RNAs in association with JY syndrome and concluded that neither viruses nor viroids were involved. R. I. Hamilton (*unpublished*) was also not able to identify dsRNA species consistently associated with this disease. In Scotland, on the other hand, four major dsRNA bands with relative molecular weights of 3.5, 2.8, 1.4, and 0.9 million daltons were found in leaf extracts of the strawberry cultivar Tyee that showed severe JY symptoms but indexed negative by leaflet graft analysis for known strawberry viruses. Parallel extractions from leaves of the strawberry cultivar Cambridge Favourite with mild or no JY symptoms did not show these major bands, and the dsRNA bands that did occur were not consistently associated with JY. Several other cultivars, both with and without JY, had dsRNA bands in the 2–4 million dalton range that appeared erratically in successive extractions but were always lacking in symptomless cultivars. Bands of dsRNA in the 0.5–1.5 million dalton range were found with greater consistency in plants showing JY than in symptomless plants (16,17). The role of dsRNA in the etiology of JY is still unclear, but it seems that no particular dsRNA profile is generally associated with JY in all affected strawberry cultivars that have been studied.

Conclusions and Outlook

ELISA detection procedures are now standard for all of the non-aphid-borne, mechanically transmitted viruses with wide host ranges that infect strawberry, for example, the nematode-transmitted viruses, tobacco streak virus, and tobacco necrosis virus (6). Active research is in progress to develop serological detection methods for several of the aphid-borne strawberry viruses (mottle, vein banding, crinkle, and mild

Fig. 5. Symptoms of strawberry latent C virus on *Fragaria vesca* cv. EMK. (Courtesy USDA-ARS)

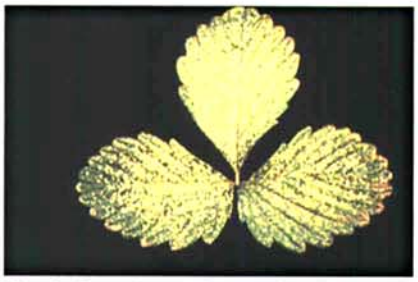

Fig. 6. Symptoms of strawberry pseudo mild yellow-edge virus on *Fragaria vesca* var. *semperflorens* cv. Alpine. (Courtesy USDA-ARS)

Fig. 7. Strawberry green petal disease symptoms on cultivated strawberry showing green flower petals and affected fruit. (Courtesy USDA-ARS)

Fig. 8. Leaf mottling symptoms caused by tomato ringspot virus on *Fragaria vesca* cv. UC-4. (Courtesy USDA-ARS)

Fig. 9. Shock symptoms (necrosis) of tobacco streak virus on *Fragaria vesca* var. *semperflorens* cv. Alpine. (Courtesy USDA-ARS)

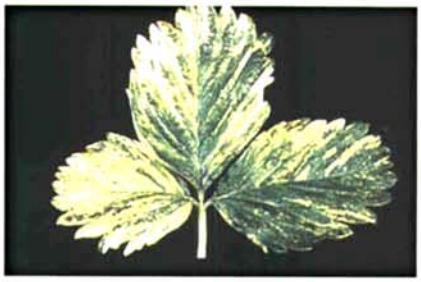

Fig. 10. June yellows on cultivated strawberry. (Courtesy USDA-ARS)

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yellow-edge) to match the success already achieved (34) with the serodetection of the aphid-borne carlavirus, strawberry pseudo mild yellow-edge virus.

Alternatively, the application of dot hybridization assays using cloned radioactive probes as diagnostic reagents has met with some success for the detection of MLOs and both RNA and DNA viruses of strawberry. The facility with which such assays have been used to detect caulimoviruses and MLOs in single insect vectors (18,28,30) suggests that such approaches may prove useful as well for epidemiological studies of vectored strawberry viruses.

Several leafhopper-transmitted strawberry disease agents other than those discussed are reported to be caused by MLOs, including witches'-broom and multiplier plant in the United States and mycoplasma yellows in Australia (6). Rapid laboratory detection procedures have not yet been reported for these MLOs or for the organism associated with rickettsia yellows in Australia (6).

The etiology of the widespread and damaging strawberry disease pallidosis has not been confirmed beyond its graft transmissibility (6). No laboratory procedures for its rapid, accurate detection have been reported. Similarly, the etiologies are unknown and rapid detection methods are lacking for two rare U.S. strawberry viruslike diseases, feather-leaf and leafroll. A half dozen other graft-transmissible disorders have been reported from strawberries, but little is known about them beyond symptomatology on grafted indicator hosts (6). Several research laboratories around the world continue to investigate the properties and methods of rapid, sensitive serological or biochemical detection of many of the important strawberry virus and viruslike pathogens.

Until the present gaps in the methodology for laboratory detection of the major strawberry virus and viruslike pathogens are closed, the practical evaluation of plant health of strawberry nursery and fruiting stocks will have to continue to depend on the traditional system of leaf grafting to sensitive *F. vesca* and *F. virginiana* Duchesne indicator plants.

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