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Mint Viruses: Beauty, Stealth, and Disease

Mint has been cultivated for thousands of years for the unique fragrances produced by its volatile oils. The genus *Mentha* contains more than 45 accepted species and subspecies (83); however, commercial production of mint oil is based primarily on *M. arvensis* L. (Corn Mint), *M. spicata* L. (spearmint), and *M. x piperita* L. (peppermint). The leading countries in mint production are India, the United States, China, and Brazil. In India, mint is cultivated in an area of more than 150,000 ha with estimated production of 15,000,000 kg of essential oil, which accounts for about 80% of the world menthol mint production (Table 1; 5). In the United States, the cultivated area is about 50,000 ha, with peppermint representing about 80% and spearmint 20% of the production area and the crop value. Oregon and Washington are the largest producers followed by Idaho, Indiana, Wisconsin, and Michigan (Table 2; 84). Other mint species also are grown widely for the food, medicinal, and landscape trades.

The USDA Agricultural Research Service (ARS) maintains a living collection of world *Mentha* germplasm at the National Clonal Germplasm Repository (NCGR), a genebank in Corvallis, OR. This collection includes 447 plant accessions and 55 seedlots representing 40 taxa with origins in 46 countries (11,85). Mint as a crop is propagated clonally, and many clones have existed for decades and probably centuries, with cuttings shared among farmers, re-

searchers, arboretums, nurseries, and gardeners. Repeated clonal propagation and wide geographic exchanges have provided abundant opportunities for viruses to accumulate in mint clones and travel the world. Much of the USDA *Mentha* germplasm collection originated with the A. M. Todd Company in Michigan, where mint breeder M. J. Murray had assembled germplasm from North America, Europe, former western Soviet Republics, and many other parts of the world from about 1950 to 1970. The Murray collection was donated to Oregon State University in 1972, transferred to the USDA in 1978, and became the base *Mentha* collection at the ARS-NCGR genebank in 1983 (11).

The involvement of three of the authors of this review with mint viruses began with the ornamental cultivar Golden Ginger Mint (GGM). “‘Golden Ginger Mint’ makes its most striking display as new growth emerges in spring, when the striations in the leaves are at their peak.” So begins a 1991 article about landscape use of mints in a national gardening magazine (65). This ornamental mint, with its golden streaks in the dark green leaves, was considered to be “one of the most striking of all mints.” GGM (Fig. 1), also marketed under the cultivar name Green and Gold, attracts the attention of many gardeners who purchase plants through nursery catalogs and at garden centers across the United States. This “variegated” mint has also attracted the attention of plant taxonomists. Tucker and Fairbrothers (75) traced the taxon *Mentha variegata* Sole to a type specimen vouchered in 1798 and described as identical to *M. x gentilis* L. “...except that the major veins are yellowed.” Tucker and Fairbrothers, however, recognized the leaf variegations as virus symptoms that they were able to transmit to healthy mint plants by grafting (Fig. 2). They proposed

correcting the taxon to *M. x gentilis* L. ‘Variegata’ which properly designates a horticultural clone (75). The taxon *M. x gentilis* has since been revised to *M. x gracilis* Sole (76). However, the former name is still used widely in the nursery industry and scientific literature. Over the 200 plus years since this virus-induced “variegated” mint was first described, gardeners and nursery industries efficiently disseminated the clone, along with its viruses, worldwide.

The *M. x gracilis* ‘Variegata’ clone (PI 557928) at NCGR attracted the attention of author Postman in 1989, and he was able to eliminate the variegation using heat therapy and meristem culture. He also induced symptoms in *Chenopodium quinoa* mechanically inoculated with sap from a variegated mint plant and observed 30-nm spherical virus particles in leaf dips by transmission electron microscopy (unpublished). More mild or transient vein banding and mosaic symptoms were also observed on other mint clones at the genebank. Efforts initiated in 2003 to isolate dsRNA from several of these plants resulted in the detection of a number of known viruses—the spherical virus isolated by Postman proved to be *Strawberry latent ringspot virus*—as well as several unknown viruses in mint summarized below (Table 3). Not all variegated mints are pathogen induced. A variegated pineapple mint (PI 557912, *M. suaveolens* Ehrh.) with white leaf margins and a variegated peppermint (PI 557974, *Mentha x piperita* L.) with striated leaves (Fig. 3) are chimeras or sports with chlorophyll mutations.

In spite of the importance of mint in many areas around the world and its use in medicine, food, and landscaping, there has not been a review of the viruses that infect these crops, a gap we hope to fill with the present article.

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Table 1. Estimated area under cultivation and production levels of oils of various mint species in India (2005–2006)^a

| Mint crop | Area under cultivation in India (ha) | Production of oil in India (kg) | Total world oil production (kg) | Major producing countries |
|-------------------------------------|--------------------------------------|---------------------------------|---------------------------------|----------------------------|
| <i>Mentha arvensis</i> | 150,000 | 14,000,000 | 19,000,000 | India, China, Brazil, USA |
| Peppermint (<i>M. ×piperita</i>) | 2,500 | 200,000 | 4,000,000 | USA, France, Brazil, India |
| Bergamot mint (<i>M. citrata</i>) | 1,200 | 150,000 | 200,000 | USA, Brazil |
| Spearmint (<i>M. spicata</i>) | 3,000 | 250,000 | 2,000,000 | USA, China, India |

^a Source: CIMAP farm bulletin 2006 (5): Menthol mint cultivation. Central Institute of Medicinal and Aromatic plants (CIMAP), Lucknow, India.

Table 2. Average annual U.S. mint oil production from 2005 to 2007^a

| Commodity | State | Hectares | kg | Value |
|------------|---------------------|----------|-----------|--------------|
| Spearmint | Idaho | 297 | 39,614 | \$1,090,667 |
| Spearmint | Indiana | 634 | 36,288 | \$939,667 |
| Spearmint | Michigan | 634 | 36,590 | \$857,333 |
| Spearmint | Oregon | 890 | 115,819 | \$3,025,667 |
| Spearmint | Washington | 4,546 | 689,321 | \$17,650,667 |
| Spearmint | Wisconsin | 391 | 22,075 | \$572,333 |
| Spearmint | Total United States | 7,392 | 939,708 | \$24,136,333 |
| Peppermint | Idaho | 6,070 | 657,115 | \$18,223,667 |
| Peppermint | Indiana | 4,155 | 223,927 | \$6,492,667 |
| Peppermint | Michigan | 324 | 14,818 | \$432,000 |
| Peppermint | Oregon | 9,038 | 932,450 | \$27,434,667 |
| Peppermint | Washington | 9,443 | 1,234,548 | \$33,952,000 |
| Peppermint | Wisconsin | 1,794 | 115,668 | \$3,197,000 |
| Peppermint | Total United States | 30,824 | 3,178,526 | \$89,732,000 |

^a Source: USDA 2008 (84). National Agricultural Statistics Service U.S. mint production data.

Nematode-Transmitted Viruses

Arabis mosaic virus (ArMV). ArMV was first described in the 1940s (66). It infects almost 100 plant species belonging to more than 28 families, causing significant losses in many crops (47). ArMV is a member of subgroup A of the *Nepovirus* genus, and the complete nucleotide sequence of ArMV (88,89) confirmed the close relationship of ArMV with *Grapevine fanleaf virus (GFLV)*, also a member of subgroup A. ArMV is transmitted in nature mainly by *Xiphinema diversicaudatum*, although there are reports of other *Xiphinema* species that can transmit the virus (74). It is often found in mixed infections with *Strawberry latent ringspot virus (SLRSV)* since the two viruses are transmitted by the same vector (47).

While investigating a 1966 outbreak of SLRSV in a red raspberry field in Scotland, Taylor and Thomas (72) surveyed weed species to determine potential virus reservoir hosts. They detected both ArMV and SLRSV in half of the 12 *M. arvensis* plants sampled. The authors collected seed from an infected plant and grew 35 seedlings. None tested positive for ArMV; however, SLRSV was seed transmitted to two of the mint seedlings. This is the only known report of ArMV in mint.

Strawberry latent ringspot virus (SLRSV). Although originally isolated from rosaceous hosts (38), SLRSV is now known to infect more than 130 species belonging to more than 30 families of both

monocots and dicots (32,62), including composite, crucifer, legume, and solanaceous hosts. A nematode-transmitted virus, SLRSV is only transmitted by nematodes in the genus *Xiphinema* (*X. diversicaudatum* and *X. coxi*) (48). This property, in addition to the seed, pollen, and effortless mechanical transmission, placed SLRSV in the *Nepovirus* and then in the *Sadwavirus* genus (46), but in light of the genomic sequence and the phylogenetic distance of the virus from any other member of the order *Picornavirales*, this classification will probably change again in the future (37,78).

Wild mints growing as weeds were reported as hosts of SLRSV in the 1960s (62,72), but there were no other reports of the virus in *Mentha* until 2004 in GGM (54). Postman, Chambers, and Stace-Smith worked on the viral etiology of 'Variegata' or GGM and were able to isolate a spherical virus from the plant (J. D. Postman, unpublished results). The virus was later identified as SLRSV (54), but it is not the causal agent of the 'Variegata' phenotype, as additional viruses were found in several 'Variegata' clones, some of which were SLRSV-free. SLRSV had quarantine status in the United States prior to 2004, with only two reports of the virus in North America. Both of these were isolated cases, one involving imported seed (3,29). After SLRSV was found in several areas of the United States and Canada (44,54), the U.S. quarantine was lifted. The presence of SLRSV in U.S. peppermint and spearmint production fields is undetermined, but the



Fig. 1. *Mentha ×gracilis* 'Variegata' (Golden Ginger Mint) from U.S. nursery source.



Fig. 2. Cleft graft used to transmit virus from scion to rootstock.

Table 3. Viruses that infect mint: name, acronym, genus, transmission, method of laboratory detection, and distribution

| Virus name | Acronym | Genus | Transmission | Detection | Distribution | References in mint |
|------------------------------|---------|-------------------------|------------------|---------------|---------------|--------------------|
| Alfalfa mosaic | AMV | <i>Alfamovirus</i> | Pollen, aphid | ELISA, RT-PCR | Worldwide | 21,25,41,50,55 |
| Arabis mosaic | ArMV | <i>Nepovirus</i> | Nematode, seed | ELISA, RT-PCR | Scotland | 72 |
| Cherry rasp leaf | CRLV | <i>Cheravirus</i> | Nematode, seed | ELISA, RT-PCR | Worldwide | 73 |
| Cucumber mosaic | CMV | <i>Cucumovirus</i> | Aphid | ELISA, RT-PCR | Europe, China | 25,28,55,86,93 |
| Impatiens necrotic spot | INSV | <i>Tospovirus</i> | Thrips | ELISA, RT-PCR | USA, Italy | 2,26,64,69 |
| Lychnis ringspot | LRSV-M | <i>Hordeivirus</i> | Seed? | ELISA | Hungary | 6 |
| Mint vein banding associated | MVBaV | <i>Unassigned</i> | Aphids | RT-PCR | Worldwide | 79 |
| Mint virus-1 | MV-1 | <i>Closterovirus</i> | Aphid | RT-PCR | USA | 80 |
| Mint virus-2 | MV-2 | <i>Vitivirus</i> | Aphid | RT-PCR | USA | 82 |
| Mint virus X | MXV | <i>Potexvirus</i> | – | RT-PCR | USA | 81 |
| Peppermint latent | PeLV | <i>Cheravirus</i> | Nematode? | RT-PCR | USA | 73 |
| Peppermint stunt | PmSV | <i>Vitivirus</i> | Unknown | Hybridization | USA | 13,14,39,40 |
| Strawberry latent ringspot | SLRSV | To be determined | Nematode, seed | ELISA, RT-PCR | Worldwide | 54,62,72,78 |
| Tobacco mosaic | TMV | <i>Tobamovirus</i> | Mechanical | ELISA, RT-PCR | India | 60 |
| Tobacco ringspot | TRSV | <i>Nepovirus</i> | Pollen, nematode | ELISA, RT-PCR | USA | 70 |
| Tomato aspermy | TAV | <i>Cucumovirus</i> | – | – | China | 93 |
| Tomato leaf curl Pakistan | ToLCPKV | <i>Begomovirus</i> | Whitefly | PCR | India | 58 |
| Tomato spotted wilt | TSWV | <i>Tospovirus</i> | Thrips | ELISA, RT-PCR | USA, Italy | 2,26,64,69 |
| Unidentified filiform | – | ? | ? | ? | Bulgaria | 34 |
| Unknown Rhabdovirus | – | <i>Cytorhabdovirus?</i> | ? | TEM | Germany | 33 |

**Fig. 3.** Variegated peppermint (PI 557974), a genetic mutation.

virus presence is highly unlikely since the two major vector species are not known to be present in the country.

Tobacco ringspot virus (TRSV). TRSV was first identified by Fromme et al. (24) and has a wide range exceeding 35 plant families of both monocots and dicots (67). The virus belongs to subgroup A of the genus *Nepovirus* (family *Comoviridae*) and is transmitted by nematodes of the genus *Xiphinema* (12,23). As a typical nepovirus, it is easily transmitted mechanically and in seed and pollen. While it can be efficiently transmitted by its vectors, it is lost when they molt, and this characteristic has been used successfully to minimize the impact of the virus in the field (52).

In 1962, Stone et al. (70) identified several stunted and rosetted *M. spicata* (American spearmint) plants with deformed leaves in an Indiana field. Plants were found in only two small areas with high populations of the vector *X. americanum* Cobb. As is the case with many viruses, and especially nepoviruses, plants remain symptomless after initial root infection and symptoms emerged in new shoots originating from infected rhizomes after the virus overwintered. Stone et al. (70) saw no TRSV symptoms on *Mentha*

cardiaca (syn. *M. ×gracilis*) plants growing near infected spearmint plants. A clone of *Mentha ×verticillata* L. (PI 558004) at NCGR exhibiting mild vein-banding symptoms tested positive for TRSV by enzyme-linked immunosorbent assay (ELISA) and reverse transcription–polymerase chain reaction (RT-PCR). TRSV has the potential to cause problems only in areas where vectors are found in abundance and mint is rotated with a crop that is a host for the virus. The vector *X. americanum* occurs in all the major mint producing areas of the United States.

Aphid-Transmitted Viruses

Alfalfa mosaic virus (AMV). AMV was first described in the 1930s (87), and it infects more than 300 species from 47 families of both monocots and dicots (31). AMV is the type and sole member of the genus *Alfamovirus* in the family *Bromoviridae* and is transmitted efficiently by a number of aphid species. Except for aphid transmissibility, it has all the characteristics of ilarviruses: tripartite genome with identical organization to that of most ilarviruses; efficient transmission mechanically, by seed and pollen; and relatively unstable particles having bacilliform virions of different lengths. The ability of AMV to be transmitted by aphids is the primary reason that it is assigned to a distinct genus. Phylogenetic analysis clearly indicates that AMV is more closely related to members of subgroups 3 and 4 of the ilarviruses than are other members of the *Iilarvirus* genus. Since there are more than 15 species in the *Iilarvirus* genus, it is plausible that AMV was a true ilarvirus until it acquired the ability to be aphid transmitted after mutations in one or more AMV genes.

A new virus disease causing chlorotic leaf spots on peppermint in Germany was

given the name peppermint pale spot in 1963, and plants infected with the virus seemed to be more resistant to rust (*Puccinia menthae* Pers.) than uninfected plants (50). Richter (55) determined that peppermint pale spot was caused by AMV and that it could be transmitted readily by several different aphid species. AMV was identified in Italy as the cause of yellow leaf symptoms and stunting in peppermint in 1963. The Italian group was able to transmit the virus by grafting but not mechanically (41). The virus was found more recently in English mint exhibiting interveinal chlorotic mottle and ringspots in New Zealand (21). The effect of AMV on the growth and essential oil content has not been studied, but the virus is found in mint in Europe (25) and New Zealand and in legumes worldwide. The efficiency of transmission of the virus makes it a potential problem for the industry, especially in situations when plants are infected with other aphid-transmitted viruses, leading to mixed infections and disease as those described in this review.

Cucumber mosaic virus (CMV) and Tomato aspermy virus (TAV). CMV is the type member of the genus *Cucumovirus*, family *Bromoviridae*, and infects more than 1,000 plant species representing more than 86 families and causes economically important diseases worldwide (51). Ever since its first report on cucumber (19), CMV has emerged as a plant virus with an ever-expanding host range (56). TAV was first described in 1949 (9) and infects at least 100 species in 24 dicotyledonous and three monocotyledonous families (30). Various strains of CMV that differ in their biological, serological, and physico-chemical properties have been isolated worldwide (51) and have been divided into two subgroups. Several aspects of the two viruses are identical as both are transmitted

efficiently by aphids in a nonpersistent manner, by seed, pollen, and mechanically.

The earliest report of CMV affecting *Mentha* was in 1966 in Germany, where it was found to be the cause of a mosaic disease of peppermint that was easily transmitted by aphids (55). Hani (28) studied the epidemiology of CMV in Switzerland and reported *Mentha* sp. as a weedy host for the virus in the vicinity of tobacco fields where several CMV isolates were causing problems. CMV and AMV were found in cultivated medicinal plants, including mint, in Hungary (25). CMV was an important pathogen of cultivated *Gladiolus* sp. in northern Italy in 1988, and a survey of weeds in production fields found infected *Mentha* spp., including *M. arvensis*, to be a virus reservoir (86). Zhou et al. (93) isolated two viruses (MS-Z and MS-S) from infected *M. spicata* plants in Shanghai, China exhibiting mosaic and distorted leaves. After mechanical inoculations, *M. haplocalyx* was also identified as a host of the viruses. Biophysical properties and morphology of the virus particles were similar to cucumoviruses. Based on host range and symptoms, properties in vitro, aphid transmission, particle morphology, and serological tests, MS-Z and MS-S were identified as CMV and TAV, respectively. This is the only record of these viruses infecting *M. spicata*.

Mint vein banding associated virus (MVBaV). MVBaV is one of two closteroviruses that infect mint. MVBaV was discovered in a 'Variegata' clone at NCGR (PI 557928) but is not the causal agent of the phenotype as it was not present in some other 'Variegata' clones. MVBaV may have played a significant role in the evolution of the *Closteroviridae* as we know it today (79). There are three genera

established in the *Closteroviridae* (43), and members of each genus are transmitted by either aphids, mealybugs, or whiteflies with only a few species of each insect taxon able to transmit a particular closterovirus. These properties, in addition to the inability of most closteroviruses to be transmitted mechanically, are probably responsible for the limited host range of viruses in the family. Several of the MVBaV proteins have almost identical phylogenetic distances from orthologous proteins of members of the three genera of the family. The virus is monopartite based on the length of the particles and the size of the genome, indicating that the common ancestor before the split of the family into the three distinct genera was monopartite. The ability of the mint aphid (*Ovatus crataegarius*) to transmit the virus provides insight into the evolution of the family, as it suggests that the last common ancestor was also transmitted by aphids. In a survey of mint fields in western Oregon ('Redefined Murray') we determined that MVBaV was prevalent in the samples tested, although no visual symptoms were associated with its presence. In contrast, several genebank accessions, including a wild-collected *M. canadensis* L. from Ontario, Canada (PI 557629) (Fig. 4), exhibited transient vein-banding symptoms and tested positive for MVBaV (79), indicating that environment and host species play a significant role in symptom expression.

Mint virus-1 (MV-1). The second closterovirus infecting mint was identified in a

mint clone obtained from a mail-order nursery as part of the 'Variegata' study. Symptoms in this clone were different from other 'Variegata' clones since typical vein-banding symptoms were absent but leaf crinkling was observed ('Oregon Ginger Mint' in Figure 5). While the clone was not 'Variegata', we examined the possibility that symptoms were of viral etiology. We isolated three viruses from this plant: TRSV, MV-1, and *Mint virus-2* (MV-2), which is described below. This mint clone was designated 'Oregon Ginger Mint' (OGM). MV-1 has similar genome organization to *Beet yellows virus*, which is the type member of the genus *Closterovirus*, the aphid-borne members of the family *Closteroviridae* (80). Phylogenetic analysis of multiple proteins and motifs showed that MV-1 is closely related to both *Beet yellows virus* and *Citrus tristeza virus*, although the latter possesses additional genes not found in MV-1. The sequence similarity with diversity in genome organization highlights the capacity for members of the family to acquire or lose genes. In the case of MV-1, there are remnants of genes found in CTV that were probably not essential as the common ancestor of the viruses moved to new hosts. MV-1 is transmitted by the mint aphid, although plants aphid-inoculated with single isolates remained asymptomatic (80). The virus has been found in production fields and in the NCGR mint collection in single and mixed infections and is typically not associated with symptoms.



Fig. 4. *Mentha canadensis* (PI 557629) infected with *Mint vein banding associated virus* and *Mint virus-1*.



Fig. 5. Oregon Ginger Mint infected with *Mint virus-1*, *Mint virus-2*, and *Tobacco ringspot virus*.

Vitiviruses

Mint virus-2 (MV-2). MV-2 was discovered in the same OGM clone as MV-1. The virus belongs to the genus *Vitivirus* in the family *Flexiviridae* and is closely related to members of the genus that infect grapevine, namely *Grapevine virus A, B, and D*. While the virus genome has not been completely sequenced, sequence information in the genomic region from the RNA-dependent-RNA polymerase to the 3' terminus shows the highest similarity to *Grapevine virus D* and *Heraclium latent virus*. MV-2 was not mechanically transmissible to 13 herbaceous indicator species but was transmitted by the mint aphid. Aphid transmission was only possible in the presence of a helper virus, presumably MV-1, as transmissions from the OGM clone were successful (15% transmission efficiency), but transmission studies using the MV-2 single isolate infected plants obtained after aphid transmission were unsuccessful (82). This is not unusual with vitiviruses, since *Heraclium latent virus* is also aphid transmissible in the presence of a helper virus (7). MV-2 is symptomless in single infections, while in the NCGR and Oregon mint field survey it was only found in association with MV-1, another indication that the closterovirus may act as the helper virus for aphid transmission.

Peppermint stunt virus (PmSV). In the early 1990s, 'Black Mitcham' peppermint plots in Oregon planted with meristem derived nursery stock were observed to grow more vigorously than plots planted with nonmeristem sources; however, the more vigorous meristemmed plants produced lower yields of mint oil (13). Double-stranded RNA (dsRNA) isolated from nonmeristem plants suggested the presence of a virus in low concentration, whereas no dsRNA was detected in meristemmed plants (14). Samples from nearby spearmint plots yielded a dsRNA banding pattern different from those in the peppermint samples (40). The virus from Black Mitcham, designated Peppermint stunt virus, was found to be related to *Grapevine virus A* (GVA) (40). Primers flanking the GVA capsid protein gene were used to amplify the PmSV capsid protein gene, which was then cloned and sequenced (40). The coat protein sequence of PmSV shares about 75% nucleotide sequence identity with MV-2 and GVA (39), demonstrating that it is a member of the genus *Vitivirus*. Dot-blot hybridization assays also revealed the presence of PmSV in symptomless spearmint field samples. The coat protein gene sequence from the peppermint and spearmint isolates of PmSV share 87% sequence identity at the nucleotide level and 91% at the amino acid level (39).

Mint growers may be hesitant to plant virus-free meristem plants if oil yield is reduced (14). The U.S. mint industry operates a certification program to provide clean nursery stock using tissue culture

propagated foundation plants, with the primary emphasis on freedom from *Verticillium* spp. However, at this time meristem propagation is avoided so as not to eliminate the "beneficial" PmSV, which increases oil yields (R. Lundy, *personal communication* 10/2008).

Thrips-Transmitted Viruses

Tospoviruses: *Impatiens necrotic spot virus* (INSV) and *Tomato spotted wilt virus* (TSWV). The ability of TSWV to infect mint is unclear, and for this reason we will discuss INSV and TSWV together. INSV and TSWV are closely related, although TSWV has a broader reported host range that includes more than 1,000 plant species. Both viruses are vectored by the western flower thrips, *Frankliniella occidentalis*. Thus, INSV was not recognized as a novel species until the early 1990s (15,16,36) and was documented as TSWV-*Impatiens* strain in the first report of the virus in mint (64). Since then, INSV has been shown to have a broad host range in excess of several hundred species ranging from herbaceous ornamentals to woody fruiting plants. INSV and TSWV belong to the genus *Tospovirus*, the only genus in the family *Bunyaviridae* that includes plant viruses. Tospoviruses also have the ability to infect insect vectors. They can infect and replicate in thrips cells and affect the insect's fitness. The viruses have three negative or ambisense genomic RNA molecules encoding five proteins that are involved in virus replication and encapsidation. They are retransmitted in a replicative, persistent manner. Virus acquisition that leads to transmission only occurs with larvae, and if acquired at this stage the virus can be transmitted for the life of the vector. Virions are transtadially passed between larval and adult stages but cannot be transmitted if acquired in the adult stage. The viruses are acquired by adult thrips but cannot move to salivary glands to be transmitted (91). INSV can be transmitted primarily by two *Frankliniella* species (*F. occidentalis* and *F. intonsa*), although the efficiency of the western flower thrips is much higher than *F. intonsa* (57). Transmission was as high as 60% in experiments with a pair of thrips (17). TSWV can be transmitted by several thrips species including members of the genera *Thrips* and *Frankliniella*.

On mint, INSV causes stunting and general decline, while TSWV pathogenicity is uncertain. In Oregon, where the viruses were identified for the first time in mint, several hundred plants were tested for what was known as TSWV at the time, and more than 30% were found infected. In the study, antisera raised against two isolates of the virus were used: the *impatiens* isolate of TSWV (now INSV), and the lettuce isolate, presumably TSWV. About half of the positive samples were detected using the *impatiens* isolate antisera and the rest

with the lettuce isolate (2). In Ontario, Canada, mint was also confirmed as a host for the tospoviruses using ELISA with antibodies developed against a chrysanthemum isolate. Chrysanthemum is a host for both viruses (69). A report from Italy also found TSWV in mint using mechanical inoculations and ELISA (26).

For INSV, the symptoms on young leaves may include bright yellow, irregular mottling, while older leaves develop irregular, brownish gray, sunken lesions (Fig. 6). Serological tests indicated highest virus titers in rhizome tissue and mature, dark green leaves showing a bright yellow mottling, while titers were generally low in stems and completely chlorotic leaves. Reports on the importance of the viruses to the mint industry are conflicting. Virus could be found in about 30% of the tested material in the study by Allen (2), but the titer later diminished to a level that could not be detected using immunological methods. The wide host range of the viruses and transmission by mechanical means in the absence of vectors makes both of these viruses potential threats to mint production.

Whitefly-Transmitted Viruses

Tomato leaf curl Pakistan virus. The genus *Begomovirus* belongs to the family *Geminiviridae* and includes viruses with one or two circular single-stranded DNA genomes encoding six or seven proteins. Begomoviruses are emerging plant viruses, due to their increasing incidence and the severity of the diseases they cause in a number of economically important crops, mostly in tropical and subtropical regions of the world (20,53). They are transmitted by *Bemisia tabaci* whiteflies, a pest that adapts to new hosts and geographical regions.

In a 2005 survey, spearmint (*Mentha spicata* cv. *Viridis*) in Lucknow and ad-



Fig. 6. *Impatiens necrotic spot virus* in mint. (Courtesy Diane Sether)

joining areas in India showed mosaic, yellowing, leaf curling, crinkling, and retarded growth that induced drastic reduction in herb yield (Fig. 7). In severely infected fields, approximately 50 to 60% of plants showed symptoms. When plants are infected at a very early stage or after transplantation, there was a total loss of biomass suitable for herbs. A begomovirus was isolated from infected plants, and sequence analysis indicated that it was an isolate of *Tomato leaf curl Pakistan virus*, sharing 93% nucleotide sequence identity with the type isolate (nomenclature according to 1, 58). Viruses belonging to the *Tomato leaf curl virus* group generally incite prominent leaf curling, cupping, reduction in leaf size, stunted plant growth, and reduced inflorescence and fruit set, symptoms similar to those observed in the mint field. Studies on the epidemiology of the disease are still in progress.

Viruses with Unknown Vectors

***Tobacco mosaic virus (TMV)*.** TMV was the first plant virus to be identified. TMV is distributed worldwide and infects over 150 species belonging to at least nine families (10). The TMV genome consists of a single-stranded RNA that encodes four proteins and is encapsidated in rod-shaped particles $\sim 300 \times 18$ nm. The virus is transmitted mechanically and occasionally by seed (through the testa, not the embryo).

Although serious diseases caused by TMV have been known for more than a century, the virus was first reported in *Mentha* growing in 1994 in India (59,60). A virus was suspected to be the cause of a mosaic disease of *M. arvensis* in India 30 years earlier, but no virus was identified (49). The 1994 report of disease symptoms in Scotch spearmint (*M. \times gracilis* Sole syn. *M. cardiaca* Baker) included mosaic, green vein banding, deformation of leaves, and poor stunted growth (Fig. 8). It was determined that symptoms were caused by an isolate of TMV based on host reaction, biological properties, mode of transmission (mechanical transmission, no vector), and electron microscopy of partially purified particles (59). Disease incidence was in the range of 20 to 30% in severely infected fields and the virus still persists in India.

***Lychnis ringspot virus-mint*.** *Lychnis ringspot virus* (LRSV) was identified in 1955 in *Lychnis divaricata* and can infect plants belonging to at least 10 families (8). LRSV belongs to the genus *Hordeivirus*, a group of tripartite positive-strand rod-shaped RNA viruses. The genome organization of LRSV is very similar to that of the type member of the group, *Barley stripe mosaic virus* (61,92).

The presence of the virus in mint and the exact symptoms it causes are uncertain. The first and only report of the virus infecting mint comes from a plant with mosaic symptoms from western Hungary (6),

and no sequence information is available for this isolate. The mint and the type isolate of the virus cross react strongly in reciprocal antisera tests, although details of these experiments were not provided in the Beczner et al. (6) study. The mint isolate had a wider host range and caused different symptoms compared to the type isolate. Those results are reinforced by the fact that the type isolate inoculations were performed in two different locations (British Columbia and California) minimizing environmental effects on infection and symptom development. Comparison of the mint and type isolate RNAs showed significant differences in agarose gels with several additional RNAs present in the mint isolate, suggesting the possibility of a mixed infection. Finally, hybridization experiments using radio-labeled probes and 100 ng of purified virion RNA in the blots, amounts that can be visualized after ethidium bromide staining, only gave a weak signal after a 20-hour exposure, suggesting a distant relationship. These experiments indicate that the mint and type isolates of LRSV are probably closely related but distinct hordeiviruses. A similar

relationship has been shown for *Strawberry necrotic shock virus* (SNSV), which was thought to be an isolate of *Tobacco streak virus* (TSV) for decades based on strong cross-reactivity of antisera for the two viruses, but they did not cross-react in nucleic acid hybridization assays. Once these two viruses were sequenced, it became clear they were related but distinct viruses (77), and a similar situation may well exist for the two isolates of LRSV.

***Mint virus X (MVX)*.** A new potexvirus, MVX, was isolated from all *Mentha* 'Variegata' clones in the Tzanetakis et al. (81) study. The MVX genome is about 6 kb, encoding five proteins, with all the typical motifs and functions of members of the genus *Potexvirus*. MVX is readily transmissible to a range of herbaceous hosts but is not efficiently (if at all) transmissible to mint since 75 clonally propagated virus-free mint plants did not become infected when inoculated mechanically with the virus, a similar situation to the one observed with AMV (41). The inability to transmit back to mint using either plant tissue or purified virus did not verify whether MVX is the causal



Fig. 7. Begomovirus in *Mentha spicata*. source.



Fig. 8. Tobacco mosaic virus in *Mentha gracilis*.

agent of the 'Variegata' phenotype, although it has been found in all 'Variegata' clones tested. MVX is closely related to *Strawberry mild yellow edge virus*, a potyvirus that is difficult to transmit mechanically but is aphid transmissible, probably in the presence of a helper virus. Trials with the mint aphid, a vector of several of the viruses our group has characterized, failed to transmit MVX and elucidate the movement of the virus in the field. A survey in the NCGR *Mentha* collection in Corvallis, OR found several clones that were singly infected with the virus (unless additional unknown viruses are also present). Phenotypes ranging from asymptomatic to the impressive 'Variegata' indicate that host species, virus isolate, or combinations of different viruses may play a role in symptomatology. Given the different phenotypes, it seems prudent to be able to induce symptoms in virus-free mint plants following inoculation with MVX before designating it as a causal agent of vein-banding symptoms.

Poorly Characterized Viruses

Peppermint latent virus (PeLV)/Cherry rasp leaf virus (CRLV). During the process of preparing an EST library from peppermint, several clones with viral sequences were identified. The virus, presumably latent in the clone used for the preparation of the library, was named Peppermint latent virus. Comparisons of regions of RNA1 and RNA2 indicate that PeLV is related most closely to CRLV and *Apple latent spherical virus* (73), with amino acid identities between different virus protein regions being less than 70%. Interestingly, there is a clone that has 93% amino acid identity (97% similarity) to the movement protein of CRLV, indicating that two *Cheravirus* members can infect mint.

Filiform virus on *Mentha x piperita*. Kacharmazov and Tanev (34) reported a peppermint plant cv. Marica (*M. x piperita*) infected by an elongated virus (475 × 12 nm) causing leaf mosaic patterns in Bulgaria. After thermotherapy, 80% of tip explants (2 to 3 mm) showed no mosaic symptoms for 2 years, suggesting that the virus does not move efficiently into meristematic tissues. This is the only information available for this virus. The size and morphology of the particles is suggestive of members of the family *Flexiviridae*, and we cannot exclude the possibility that this is one of the viruses described above.

Rhabdovirus on *Mentha x piperita*. Rhabdoviruses infect invertebrates, animals, and plants and have important consequences for human health, agriculture, and wildlife ecology. Virions are bullet-shaped or bacilliform particles of 45–100 × 100–430 nm and have negative-sense, single-stranded RNA genomes of about 11 to 15 kb.

Intert and Amelunxen (33) observed characteristic rhabdovirus-like particles in the leaf and root cells of *Mentha x piperita*.

The plants were infested with the aphid *Myzus persicae*. Rhabdovirus particles were accumulated in the perinuclear space of parenchymatous cells of leaf vascular bundles or in procambium cells of the mesophyll and in lateral roots, respectively. Based on the characteristic morphology and the specific localization in the cell, the particles were identified as those of a cytorhabdovirus. Rhabdoviruses had been reported previously in *Tymus x citriodorus* (63) and in *Leonurus cardiaca* (22) in the family *Lamiaceae*, but this is the only report in *Mentha* sp.

Conclusions

After reviewing the literature on viruses that infect mint, it is clear that many of these viruses are latent in mint when present in single infections, which provides a perfect avenue for these viruses to be long-distance travelers assisted by man. Since mint is a minor crop with few obvious virus symptoms, there has not been a concerted effort to develop certification programs for the production of virus-tested materials as has occurred in many other vegetatively propagated crops (27). Many vegetative crops have associated latent viruses that can lead to synergistic interactions in mixed infections (42,45,71). Vegetatively propagated crops provide opportunities for mixed infections to occur over long periods of time, since viruses in any particular cultivar or clone are not subjected to the virus transmission bottleneck that occurs during pollination and seed development. In addition, an infected plant or plant propagule can be moved to new areas where it can acquire additional viruses, and this cycle can be repeated. This accumulation of viruses during vegetative propagation is probably best known in grapevine (42), strawberry (45), and citrus (90) but is true for most vegetative crops that have been cultivated for centuries.

In the work with PeSV, Crowe et al. (13) reported reduced oil production from plants that had been meristemmed compared to nonmeristemmed plants of Black Mitcham. They also showed that the meristemmed plants initially were more vigorous, but yielded less oil on a vol/wt basis and gradually lost their advantage on vegetative growth but continued to produce less oil. They suggested that the meristemming process likely resulted in plants with reduced virus titer, which over a period of 2 to 3 years returned to the premeristemming levels. It is unclear why the oil production did not return to normal if the change was due to PeSV titers and the virus was detected in these plants at the end of 3 years. When potatoes were initially freed of latent viruses, growers were reluctant to grow the plants because of increased vegetative growth and reduced tuber production. However, with modified agronomic practices, it was found that potatoes free of the latent viruses out-produced paired

infected plants with fewer inputs (4). It was suggested that cultural methods may need to be altered to take full advantage of virus-free plants (68). Another possible explanation is that the original Black Mitcham plants were infected with a second virus, such as one of the closteroviruses described above. It is known that closteroviruses have strong suppressors of gene silencing and in mixed infections can lead to increased titers of other viruses (18), which has been seen in sweet potato (35) and blackberry (71). It would be interesting to re-examine the Black Mitcham plants for possible mixed infections.

With the recent advances in virus detection, it is now possible to quickly identify viruses in field plants, whether in single or multiple infections. Certification programs for many crops worldwide are adopting these newly developed tests. The number of viruses known to infect mint has increased significantly in the last five years, and it may be time to consider virus certification for the crop. In addition to the potential for increasing yields and the longevity of plantings, such a program would reduce the risk of moving viruses into new environments with novel vectors that could lead to serious diseases in mint, other horticultural or agronomic crops, or native vegetation.

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Dr. Tzanetakakis obtained his B.Sc./M.Sc. in soil science and agricultural chemistry from the Agricultural University of Athens, Greece. His interest in plant pathology led him to the laboratory of Dr. Panayota Kyriakopoulou, where he worked on detection methods for vegetable viruses. He continued his studies in molecular and cellular biology at Oregon State University with Dr. Robert Martin, working on the characterization and epidemiology of viruses of small fruits, vegetables, and mint. After holding postdoctoral positions with Dr. Martin and Dr. Theo Dreher at Oregon State University, he moved to the University of Arkansas at Fayetteville, where he is currently an assistant professor in the Department of Plant Pathology.

Joseph D. Postman

Joseph Postman is the grandson of a New Jersey grape and chicken farmer. He grew up in the Maryland suburbs of Washington, DC and received his B.Sc. in botany from the University of Maryland. He then moved to Oregon, where he earned an M.Sc. in plant pathology from Oregon State University. He has worked at the USDA-ARS National Clonal Germplasm Repository in Corvallis since 1981, where he presently curates the living collections of pear, hazelnut, quince, and other tree crops and oversees virus testing.

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Robert R. Martin

Dr. Martin received his B.Sc. in forestry and Ph.D. in plant pathology from the University of Wisconsin-Madison. His postdoctoral experience was working with strawberry viruses at the USDA-ARS in Corvallis, OR with Dr. Richard Converse. He then joined the staff at Agriculture Canada in Vancouver, British Columbia, where he worked on small fruit viruses and *Potato leafroll virus*. He returned to the USDA-ARS Horticultural Crops Research Laboratory in Corvallis as a research plant pathologist and continues to work on viruses of small fruit crops and some viruses of ornamentals. He currently serves as research leader for the unit and is a courtesy professor in the Department of Botany and Plant Pathology at Oregon State University.