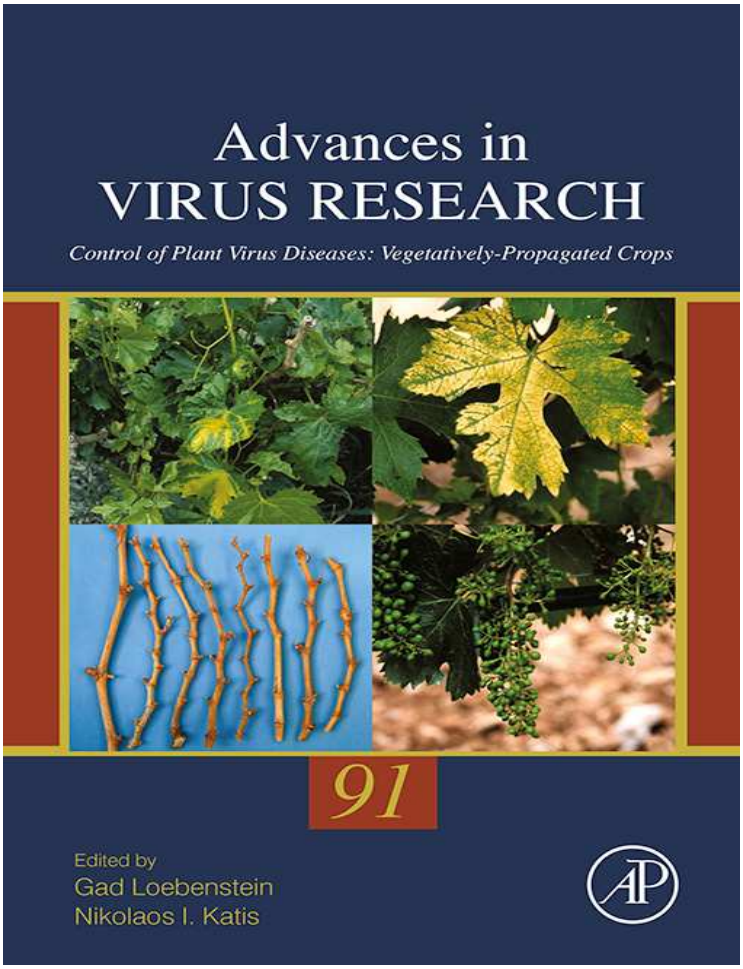

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CHAPTER EIGHT

Control of Virus Diseases of Berry Crops

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Contents

Abstract

Virus control in berry crops starts with the development of plants free of targeted pathogens, usually viruses, viroids, phytoplasmas, and systemic bacteria, through a combination of testing and therapy. These then become the top-tier plants in certification programs and are the source from which all certified plants are produced, usually after multiple cycles of propagation. In certification schemes, efforts are made to produce plants free of the targeted pathogens to provide plants of high health status to berry growers. This is achieved using a systems approach to manage virus vectors. Once planted in fruit production fields, virus control shifts to disease control where efforts are focused on controlling viruses or virus complexes that result in disease. In fruiting fields, infection with a virus that does not cause disease is of little concern to growers. Virus control is based on the use of resistance and tolerance, vector management, and isolation.

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1. INTRODUCTION

The term berry (small fruit) refers primarily to the genera *Fragaria* (strawberry), *Rubus* (blackberry, raspberry, and their hybrids), *Vaccinium* (blueberry and cranberry), *Ribes* (currants and gooseberry), and *Sambucus* (elderberry). Traditionally, berry crops have been collected from the wild at the dawn of the human species and only recently they have become agricultural crops, especially after the development of the modern strawberry (*F.* x *ananassa*). In a short period of time and because of their ever growing popularity with consumers, berry crops have been developed to grow across the globe from subtropical to subarctic environments. The major expansion in production and the environments where these crops are grown, along with the rapid changes in the genotypes grown commercially, have resulted in a very diverse virosome in berry crops (Martin, MacFarlane, et al., 2013; Martin, Peres, & Whidden, 2013; Martin, Polashock, & Tzanetakis, 2012; Martin & Tzanetakis, 2006). Those changes and the development of new technologies allowing for the rapid discovery of new viruses have led to a substantial increase in the number of known berry viruses, which has more than doubled in the last 20 years. The number of new discoveries still increases with more than eight berry viruses identified in each of the last 3 years (Martin et al., 2012; Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Martin et al., unpublished; Tzanetakis et al., unpublished). This communication aims to provide a general overview of how basic knowledge on berry viruses can be used for efficient virus control during the propagation process and field establishment.

There are more than 80 species in 30 virus genera known to infect the major berry crops (here we will only present the ones communicated in peer-reviewed publications as of May 2014). Most viruses identified before the 1990s are well-studied at the molecular and biological level, whereas, newly identified viruses are characterized primarily at the molecular level. This has led to knowledge gaps that need to be addressed. For the purpose of this communication, we will provide control strategies for those less-studied viruses based on their taxonomic placement and the accumulated biological knowledge on closely related viruses. Based on molecular data, the best guesses of potential vectors need to be considered, ranging from whiteflies to eriophyid mites to fungi. The number of vector taxa in a particular area may be such that control of all vectors is unfeasible. In general terms, areas with tradition of berry production have a set group of viruses of

concern. In most cases, there is the know-how on viruses/vectors and their control, whereas new production areas tend to have a wider array of viruses, many of which have only recently been discovered. A list of viruses infecting each of the major berry crops, their mode of transmission and their geographic range (where known) are presented in individual tables. Aphids are major virus vectors for all berries crops. They are abundant at the traditional production areas in the temperate regions around the world and just a few years ago they were considered the only vector of concern for most production areas. In most crops, the prominent aphid species colonizing the crop are also the major vectors, able to transmit an array of viruses that tend to act synergistically to cause disease as in the case of strawberry decline or raspberry mosaic (Martin & Tzanetakis, 2006; Quito-Avila, Lightle, & Martin, 2014). Notwithstanding, there are opportunistic feeders that may transmit without colonizing plants (*Myzus ornatus*; Lowery, Bernardy, Deyoung, & French, 2008). When an aphid species is crop-specific, control can be achieved through chemical sprays or even more efficiently, in the case of strawberry with crop-free times, an applicable practice for nurseries that are not neighboring commercial fields.

Nematode-transmitted viruses can cause significant losses and even plant death (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Martin et al., 2012; Martin & Tzanetakis, 2006). The major viruses infecting berry crops belong to the genus *Nepovirus* and the unassigned *Strawberry latent ringspot virus*. One of the major caveats with members of this group is their wide host range that extends to several common weeds present in berry fields. As nematode movement is restricted to less than 2 m/year, they have been successfully controlled with the use of potent nematicides such as methyl bromide. With the phase-out of the more efficient nematicides, this virus group may reemerge; especially, in areas where the nematode vectors are endemic.

Pollen and seed-transmitted viruses (PSTVs) present the most challenging group when it comes to control because the only viable control method is avoidance. In many cases, PSTVs cause significant losses in single or mixed infections whereas several of them infect multiple berry crops (MacDonald, Martin, & Bristow, 1991; Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Pallas et al., 2012). Some of the PSTVs do not have an active vector and can move passively by wind currents and pollinating arthropods such as bees, thrips (Sdoodee & Teakle, 1987), and mites, whereas others may have insect or nematode vectors, in which case control of their primary vectors can significantly reduce spread.

Whiteflies have only been identified recently as virus vectors in berry crops although there have been diseases, first reported in the 1950s, that have now been proven to be caused by whitefly-transmitted viruses (Tzanetakis et al., 2004; Tzanetakis, Wintermantel, & Martin, 2003). The emergence of this virus group as a major limiting factor to production is primarily due to the expansion of berry production to the subtropics and the extension of the geographic range of whiteflies to the temperate regions around the world. Notwithstanding, the number of whitefly-transmitted viruses is still limited and only includes species that infect strawberry and blackberry. In all cases, those viruses do not cause high-impact symptoms in single infections but act synergistically with other viruses in mixed infections to cause detrimental symptoms that can even lead to plant death (Martin & Tzanetakis, 2013; Susaimuthu, Tzanetakis, Gergerich, Kim, & Martin, 2008; Susaimuthu, Tzanetakis, Gergerich, & Martin, 2008). This should be a concern for certification programs and for nursery systems where quite often disease evaluation is based on visual observations. With many viruses of the berry crops, plants infected with one or two viruses may be asymptomatic in nursery plants and pass visual inspections, but when moved to production fields and infected with additional viruses they can decline rapidly (Martin & Tzanetakis, 2013).

Virus-vectoring eriophyid mites were discovered recently in berry crops although some of the diseases they are associated with have been reported since the beginning of the twentieth century (Jones, Gordon, & Jennings, 1984). The lack of knowledge on the biology of these vectors and the absence of systemic miticides make vector control challenging. To date, most berry mite-transmitted viruses belong to the genus *Emaravirus* (Hassan, Keller, Martin, Sabanadzovic, & Tzanetakis, 2013; McGavin, Mitchell, Cock, Wright, & MacFarlane, 2012), viruses that appear to be localized at the mite feeding sites, but there are indications that several new berry-infecting systemic RNA viruses are also mite-transmitted and involved in important diseases, primarily as part of virus complexes (Sabanadzovic, Abou Ghanem-Sabanadzovic, & Tzanetakis, 2011). A major exception is *Black currant reversion virus* (BRV), which taxonomically belongs to the genus *Nepovirus* but is transmitted by the black currant gall mite (Susi, 2004). BRV exemplifies the need for experimental verification of a virus vector as predictions based on molecular data and taxonomy may be deceiving.

Leafhoppers are another group recently identified as potential virus vectors for berry crops. To date, there are at least four blackberry viruses in the

genus *Marafivirus* (Sabanadzovic & Abou Ghanem-Sabanadzovic, 2009; Sabanadzovic, Ghanem-Sabanadzovic, & Gorbalenya, 2009; Sabanadzovic et al., unpublished), and other viruses in this genus are known to be transmitted by leafhoppers. A study in the southeastern United States identified about 50 leafhopper species in production fields (Johnson et al., unpublished), indicative of the complex virus/vector interactions that need to be elucidated before the development of meaningful control strategies.

The only thrips-transmitted virus known to infect berry crops is *Impatiens necrotic spot virus* (INSV), detected in blackberry (Tzanetakis, Guzmán-Baeny, VanEsbroeck, Fernandez, & Martin, 2009). There is no detailed work performed on transmission of the virus in blackberry that would elucidate the efficiency of transmission or the thrips species that are the primary vectors of the virus in blackberry. However, the excessive number of thrips found in several fields and the low numbers of INSV-infected plants indicate rather inefficient transmission probably because of the thrips composition in blackberry fields, or the presence of diverse flora in many blackberry fields in the southeastern United States.

A new insect group was recently added in the list of berry virus vectors. After the discovery of *Blackberry vein banding associated virus* (BVBaV; Thekke-Veetil et al., 2013), a member of the genus *Ampelovirus*, experiments were performed with mealybugs that colonize plants and successfully demonstrated transmission (Sabanadzovic et al., unpublished). As is the case with several of the berry viruses, BVBaV does not appear to cause symptoms in single infections but is often found in mixed virus infections in declining plants.

The last virus group with a single representative in the list of berry viruses to date is that transmitted by fungi. Blueberry mosaic is a disease that was first described about 60 years ago and only recently was a virus associated with the disease, *Blueberry mosaic associated virus* (BlMaV). BlMaV belongs to the genus *Ophiovirus* and has been detected in all plants with typical disease symptoms (Thekke-Veetil, Ho, Keller, Martin, & Tzanetakis, 2014). Transmission experiments are underway, and the virus is hypothesized to be transmitted by members of the genus *Olpidium*, as is the case with other members of the genus.

2. VIRUS CONTROL DURING PLANT PROPAGATION

All berry crops are clonally propagated. Breeders perform crosses and evaluate progeny annually until they identify and select plants with the

desired attributes. This process normally takes three to seven or more years depending on the crop. The selection process is usually performed in the same fields with little or no rotation leading to the establishment of viruses that circulate within the system year after year. This may the underlying reason for the tolerance present in the majority of modern berry cultivars to most single virus infections as susceptible progeny do not progress to the next selection level. However, plants in a breeding program that are grown for multiple seasons in the field in close proximity to field plots of the same crop of multiple ages are likely to be infected with one or several viruses during the selection process. This is where virus testing combined with virus clean-up programs are used to ensure that plants of new cultivars are free of targeted viruses and virus-like pathogens. These "clean" plants then enter into certification schemes to ensure the propagation of elite material with full potential for productivity and longevity in commercial fields.

3. DETECTION

Virus detection is the first step in the quest for plants that are free of targeted viruses. For the majority of the virus species that infect berry crops, there are rapid, sensitive laboratory tests available. Most viruses can be tested using molecular (polymerase chain reaction (PCR) and variants of PCR, loop-mediated isothermal amplification (LAMP), rolling circle amplification for DNA viruses, etc.), biochemical (nucleic acid hybridization, dsRNA isolation), or immunological (enzyme-linked immunosorbent assay (ELISA) in multiple formats, immunoblots, etc.) tests. In general terms, molecular tests are most widely used for newly discovered viruses, whereas immunological tests are applied to viruses where there are good-quality antibodies available. Still there are viruses or virus-like agents without laboratory tests available. In those cases, grafting onto indicators, an approach developed before the development of any of the aforementioned laboratory-based tests, is used to test for the presence of virus. Indicator plants are usually older cultivars or clones, which exhibit a range of symptoms when infected with one or more viruses. The selection of the indicators was done at a time when a subset of the viruses that infect berry viruses were known to exist and several of them are actually clones infected with an asymptomatic virus that develops symptoms when grafted with material infected with additional viruses. *Fragaria vesca* clone EMC, is infected with *Strawberry crinkle virus* (SCV) and has been used widely as a highly sensitive indicator for other strawberry viruses (Frazier, 1953). Many of the recently discovered berry

viruses are asymptomatic in the established indicators used for berry crops (Susaimuthu et al., 2007). Probably, one of the reasons that those viruses remained unidentified until the development of generic techniques that allow virus identification even in plants that lack any obvious symptoms.

Today, we have tools available that allow for virus detection and identification without any previous knowledge of the molecular, biochemical, or immunological properties of the virus. The development of macro- and microarrays with several hundreds or thousands of probes allows for the hybridization and subsequent identification of viruses with only marginal homology to known taxa (Agindotan & Perry, 2007; Thompson et al., 2014; Wang et al., 2002). Arrays present a powerful tool, allowing for broad spectrum detection of known and unknown viruses, but they may miss viruses that do not show homology with established taxa, and thus not hybridize to sequence-specific probes. This issue can be overcome with the use of next-generation sequencing as a tool for virus detection and identification (Barba, Czosnek, & Hadidi, 2014). Material can be processed using an un-bias approach where nucleic acids are amplified and analyzed for detection of known viruses and discovery of new viruses. Even when a virus does not have significant homology to established taxa, bioinformatics and structural analyses of putative proteins can lead to the discovery of previously unknown agents (Ho & Tzanetakis, 2014). This new technology is powerful and in use for the delivery—for the first time—of virus-free plants. It has been shown to be effective in multiple cases, but its implementation as the sole detection platform will require careful evaluation to ensure that it is at least as good as other methods currently in use. It will be some time before national regulatory agencies, the Regional Plant Protection Organizations, and the International Plant Protection Organization agree that these new technologies are acceptable to meet the phytosanitary testing requirements for intra- and international trade.

4. CERTIFICATION SCHEMES

Certification programs for berry crops aim to safeguard plant material during the vegetative propagation of millions of plants from a single plant to provide the best-quality planting stock to growers that have full potential for sustained production over many years. From a nursery's or fruit grower's standpoint, economics are the driving force to ensure viability and profitability. Thus, the nursery owner and fruit grower have a vested interest in certification standards that are scientifically sound in terms of disease

control, biologically doable in terms of producing high-quality plants, and economical in terms of producing high-quality plants at a reasonable cost per plant. Here, we outline state-of-the-art certification standard for berry crops based on ongoing work on *Rubus*, blueberry and strawberry certification schemes in the United States.

All cultivars start as a cross of two parents with desirable properties. Hundreds or thousands of seedlings go through rigorous evaluations before an individual is selected as a potential new cultivar. Because of the long evaluation process, many, if not all plants are infected with one or more viruses, by the time they are selected. During the last few years, with the development of new powerful technologies, the processes to obtain plants clean from all targeted pathogens have changed. Traditionally, material has been grafted onto virus-susceptible indicators. Today, in addition to grafting, advanced selections are also evaluated using molecular and serological assays and very recently next-generation sequencing (Barba et al., 2014). Data are fed into a bioinformatics pipeline that identifies all known virus sequences (detection) or even discover new viruses (Ho & Tzanetakis, 2014). After heat/chemo/cryo-therapy and meristem tissue culture (covered elsewhere in this communication), the regenerated plant is tested again for all targeted pathogens. The term "targeted" is important when accessing the economic feasibility of virus-clean-up. Several viruses may not be pathogenic, e.g., cryptic or amalgaviruses, which may be ubiquitous in specific cultivars, species, or genera of plants. These viruses lack a movement protein and appear to be present in every cell of the plant, are seed transmitted at a rate of 100%, and are not graft transmissible. These viruses have not been eliminated by any type of therapy, and their presence is not known to cause any pathology either when present alone or to have an interaction with other viruses that infect the plants. These viruses should not be included in quarantine or certification programs, thus the use of the term targeted viruses or pathogens.

When free of all targeted pathogens, the material is designated as Generation 1, or G1, and becomes the top-tier plant in a certification scheme and is the ultimate source for each plant of this cultivar. The elite material (G1) is maintained in designated vector-free facilities (screenhouses, screened greenhouses) that are free of any other plant species. The G1 plants are maintained in pots and not allowed to be in direct contact with soil to avoid soil-borne vector movement, and the plants are deflowered to minimize the risk of infection by pollen-borne viruses. Plants are tested regularly for all targeted pathogens to assure their health status.

Propagation material (cuttings, stolons, etc.) from G1 plants can be used to increase the number of plants within the same facility, but if moved off-site the material is automatically designated as Generation 2 (G2). They can be reassigned the designation G1 after being tested following establishment in the new location and found free of targeted pathogens. This material can be maintained in tissue culture, in screenhouses/screened greenhouses, or the field as long as appropriate phytosanitary conditions as defined in a certification standard are met (soil barriers to eliminate nematode movement, weed-free areas and deflowering where possible to minimize infection by pollen-borne viruses, etc.). All materials other than that in tissue culture are tested regularly (normally every 3 years), as defined in the certification standard for all major circulating viruses in this particular region ("canary" viruses). If found free of targeted pathogens, the G2 plants may continue serving as material for the next-propagation steps, whereas if the testing regime timeline is lapsed, they are eliminated from the propagation scheme. The requirements for G2 plants grown in the field are more stringent and require a higher level or frequency of testing for the "canary" viruses. Infection of G2 material leads to plant discard.

Propagation material obtained from G2 plants is designated as Generation 3, or G3, and they are normally grown in the field. The general rules applied in field-grown G2 plants also apply for the G3 plants including testing. Given the higher number of plants at this level, it is usually not feasible/economic to test all plants for "canary" viruses. For this reason, testing using a hypergeometric distribution model (ISPM No. 31) that would detect a 1% infection with 95% confidence is recommended, but may vary depending on the certification standard. Depending on the size of the block tested, if infections exceed the threshold level of 1% the block can be subdivided to smaller blocks, all of which need to be tested based on the same threshold level to identify and remove infection hotspots.

Generation 4, or G4, is the last certification level and includes all plants that are propagated for sale to fruit growers, certified plants. All rules applicable for G3 plants are also relevant for G4s, but the virus infection threshold is relaxed to identify major problems in the system that may lead to a virus epidemic. In the United States, blueberry and *Rubus* certification schemes aim to identify infection rates of more than 5% with 95% confidence. If infection exceeds the G4 threshold, subplots can be sampled to identify blocks that meet the standard. The plants from infection hotspots will not be given a certification tag and cannot be sold as certified plants.

5. GENERATING AND TESTING G1 PLANTS

The key to developing and implementing an effective certification program is to start with plants of the highest possible health status. In the United States, "Clean Plant Centers" for berries, grapes, tree fruits, and citrus have evolved since the mid-twentieth century (Gergerich et al., 2015). The role of these centers has been to produce and maintain the G1 plants. For many years, these centers were funded through a combination of fees, funding from grower organizations, and grants. In 2008, the National Clean Plant Network (NCPN) was established as part of the Farm Bill, which has led to more stable baseline funding for these programs with the goal of developing and maintaining G1 plants. Additionally, the NCPN is to provide an avenue for the introduction of cultivars into the United States that includes testing, and clean-up if necessary, with the aim of reducing the introduction of pathogens that could threaten domestic production or natural environments. There are currently two funded Centers that focus on producing the G1 plants for berry crops in the United States. The G1 collections are often maintained by state or federal agencies or some private/government arrangement. Additionally, some large, private, vertically integrated berry companies produce and maintain their own proprietary G1 plants, though the testing needs to be done or confirmed by a third party. As outlined above, certification schemes for berries crops start with a single plant that is fully tested and found free of targeted pathogens, which usually includes all viruses known to infect the crop, as well as phytoplasmas and some systemic bacteria. For the berry crops, these G1 plants are maintained in protected culture, either screenhouses or screened greenhouses.

Plants that enter into G1 collections come from multiple sources including new cultivars developed in breeding programs, cultivars in use commercially that have not been tested for all viruses of the crop, heritage cultivars that are from various collections, cultivars entering from another country. Before any plant receives G1 status, it must go through extensive testing to ensure that it is free of viruses and other systemic pathogens identified in the certification standard (Fig. 1). For materials coming from a foreign or domestic clean plant program, the plants are immediately put into the virus testing program. First, all laboratory tests are run and if all negative, the bioassays are performed. If the bioassays are all negative, the plants are ready for release. This may require submission of the test results to the regulatory body responsible for plant importation into the country to get final approval for release of the plants from foreign sources for commercial production.

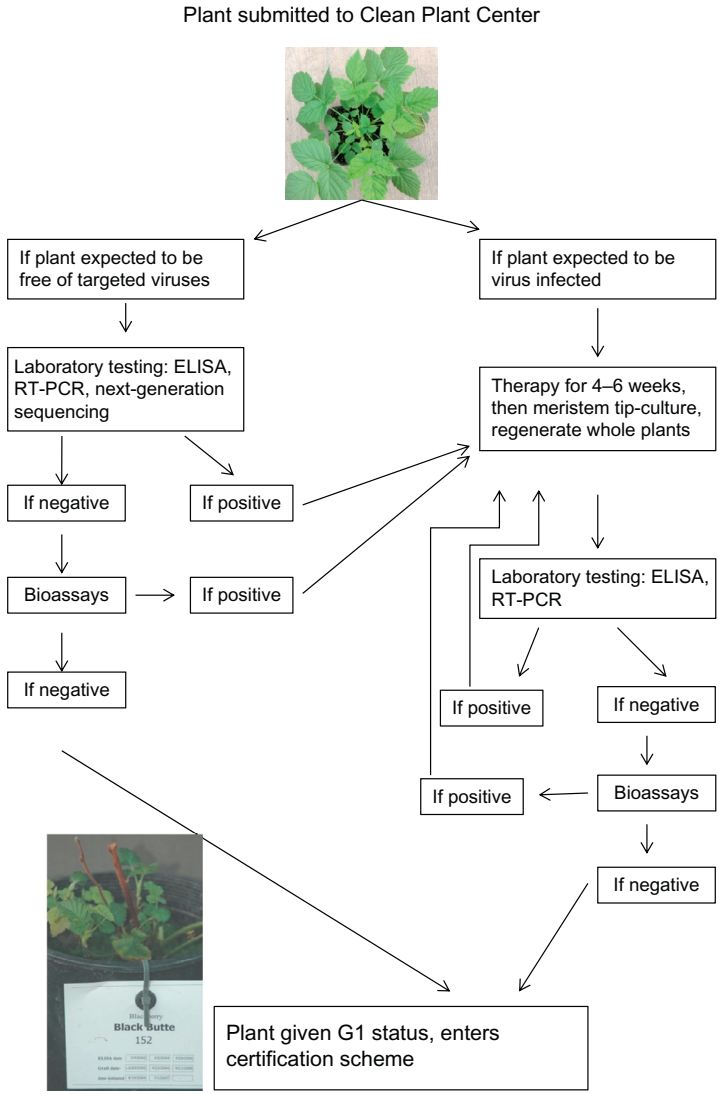

Figure 1 Path of a plant submitted to a Clean Plant Center from submission to obtaining G1 status.

Based on experience with viruses and plants from the various regions within the United States, domestic materials coming from breeding programs can follow one of several paths when received by the Clean Plant Center. For example, due to disease pressure, blackberry plants from the breeding program in Arkansas have a very high chance of being infected and enter directly into the clean-up process on arrival. This is also true

for raspberry plants coming from the breeding program in Washington State. In contrast, blackberry and raspberry plants from the breeding program in Oregon have a greater than 50% chance of being free of targeted pathogens and enter into the virus testing program when they arrive at the clean plant facility in Corvallis, Oregon. In the case of strawberries, all plants received from breeding programs are subjected to therapy and meristem-tip culture when they arrive since the disease pressure is high in most growing areas in North America for at least several of the common strawberry viruses. Having information on the prevalence of viruses by region that infect a crop helps inform decision making on what type of action to implement when new material arrives at a Clean Plant Center. This information is also used in developing the list of "canary viruses" that are the primary focus of certification programs at the G2, G3, and G4 levels. As an example, canary viruses for blueberry certification in the Pacific Northwest of the United States would be different from those in the southeastern United States.

Plants that enter into the virus clean-up process are established in large pots or in tissue culture. Then these plants (potted or tissue culture) are subjected to therapy (heat-, chemo-, or cryo-) for a period of 3–8 weeks. Then meristems, generally 0.5 mm or less are removed, grown in tissue culture until rooted, and finally potted and maintained in a screened greenhouse. At this point, plants are removed from tissue culture and potted, and a few leaves are removed for virus testing by ELISA, RT-PCR, or PCR. If any of these tests are positive, the plants are subjected to a second cycle of therapy and the process repeated. If the laboratory tests are all negative, the plants are grown until large enough for biological indexing. At this time, the plants are grafted onto indicators and retested by ELISA, RT-PCR, or PCR. If all tests are negative, the plants enter the G1 collection; if any positive tests are obtained, the clean-up cycle is repeated. Each cycle from beginning of therapy to complete testing of plants in bioassays takes about 2 years for *Rubus*. Therefore, if a positive test is obtained, the clean-up process can take 4 or more years. For this reason, we work with breeders to obtain their top selections 2 years before they are ready to name and release them as cultivars, with the goal of having G1 plants available at the time of the cultivar release. This means that we often get three to five plants into the clean-up process for each cultivar that is released. If the breeder makes a decision to drop one of the advanced selections, they work with us so that we can drop it from the clean-up process. With this cooperation, the breeders are able to release new cultivars without waiting to have a G1 source available. From the time of submission to the Clean Plant Center

until all testing is completed and plants are found free of targeted pathogens, they are considered candidate G1 plants. Once they have indexed negative in the full suite of tests required in the certification standard, they become G1 plants. Figure 1 shows the path of a plant entering a Clean Plant Center until it obtains G1 status in the certification scheme.

There is a common misconception by growers and many researchers that the use of tissue culture for plant propagation will result in plants free of viruses. *This is not true*. Tissue culture for plant propagation generally uses large tissue pieces, and plants are not subjected to any therapy treatment before hand. It would be very rare for plants to escape virus infection through routine tissue culture multiplication.

6. VIRUS CONTROL IN BERRY CROPS

For berry crops, as with any of the vegetatively propagated crops, there are two strategies for virus control depending on what product is being produced. For plant production, which includes all nursery systems, the objective is to control all targeted viruses in the crop to ensure production of plants with highest health status possible. Control of viruses at this level ensures that trade in berry plants does not result in movement of viruses to new locations, which can lead to increased vector management costs and thus production costs should a new virus be introduced. It has been shown that starting with clean plants results in better establishment and production than virus-infected plants (Quito-Avila, Lightle, & Martin, 2014). Also, virus-infected plants in a nursery setting may appear healthy, but digging, shipping, and replanting puts the plants under significant additional stresses that can lead to poor establishment and fruit production from these virus-infected plants (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013). The second type of virus control is used by fruit growers, where disease control is the objective rather than virus control. In these situations, latent viruses or mild viruses may have minimal impact on fruit production. Also, with the berry crops, most virus diseases are caused by mixed infections, thus, rather than controlling all viruses it is much more efficient to control one or two viruses that are critical for disease development. In cases where fields are established with plants carrying a symptomless virus, the addition of a second virus could lead to reduced yields or quality in the fruiting fields, thus, the importance of nurseries managing viruses rather than virus diseases.

7. VIRUS CONTROL IN NURSERIES

The viruses that have been reported to infect each of the major berry crops are shown in Tables 1–5: strawberry (Table 1); raspberry and blackberries (Table 2); blueberry and cranberry (Table 3); currants and gooseberry (Table 4); and elderberry (Table 5). The virus genera, means of transmission, detection methods, and distribution at a very large scale are also shown in these tables. Virus distribution in many cases is listed as N/A, which means the testing has not been done at a large scale and the presence or absence of the virus is not known. Also, note that the distribution is on a very large (continental) scale and for making management decisions a finer scale is much more useful. As an example, the presence of aphid-transmitted strawberry viruses in Africa and North America does not provide enough detail to make management decisions in Morocco or Florida, respectively. Information on virus distribution on a smaller scale is needed to make management decisions for a nursery or fruit grower. As an example, Raspberry leaf curl virus has been reported in eastern North America but not in west of the Rocky Mountains (Stace-Smith & Converse, 1987). Thus, management for this virus in the western United States is not a concern other than testing germplasm that comes from areas where the virus occurs, whereas, if managing this virus on the basis of its occurrence in North America, there would be resources and chemicals used for controlling this virus in the western United States There are similar cases in blueberry and blackberry, *Blueberry necrotic ring blotch virus* and most of the viruses involved in blackberry yellow vein disease occur in the southeastern United States but have not been detected in the western parts of the country. The better information available on the distribution of the viruses and their vectors, the more informed decisions growers can make on disease management.

Virus control in nurseries is based on Best Management Practices (BMPs) combined with testing. BMPs are predicated on knowing the viruses and their vectors that occur in the area where the nursery is located. If nurseries are receiving G1 plants that are free of targeted pathogens, then the nursery's objective is to prevent infection of these plants during the plant multiplication cycles. If done by conventional propagation this process may take 3–5 years, during which the plants are grown in a field setting and exposed to virus vectors and possible virus infection. In cases where tissue culture propagation is used, thousands or millions of plants can be produced in tissue culture without exposure to vectors. These tissue culture plants can then be

Table 1 List of viruses known to infect strawberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Apple mosaic	ApMV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR[a]	Yes	Yes	Yes	Yes	Yes	Yes
Arabis mosaic	ArMV	*Nepovirus*	Nematodes/semi-persistent[b,c]	ELISA, RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Beet pseudo-yellows	BPYV	*Crinivirus*	Whiteflies/semi-persistent	ELISA, RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Cucumber mosaic	CMV	*Cucumovirus*	Aphids/ nonpersistent	ELISA, RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Fragaria chiloensis cryptic	FCCV	*Alphacryptovirus?*	Pollen/seed[d]	RT-PCR	No	Yes	N/A	N/A	N/A	N/A
Fragaria chiloensis latent	FClLV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR	Yes	Yes	N/A	N/A	N/A	N/A
Raspberry ringspot	RpRSV	*Nepovirus*	Nematodes/semi-persistent	ELISA, RT-PCR	No	No	Yes	N/A	Yes	No
Strawberry chlorotic fleck	SCFaV	*Closterovirus*	Aphids/semi-persistent	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Strawberry crinkle	SCV	*Cytorhabdovirus*	Aphids/persistent	RT-PCR	Yes	Yes	Yes	N/A	Yes	Yes

Continued

Table 1 List of viruses known to infect strawberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale—cont'd

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Strawberry latent C	SLCV	*Nucleorhabdovirus*	Aphids/persistent?	N/A	Yes	N/A	N/A	N/A	N/A	N/A
Strawberry latent ringspot	SLRSV	Unassigned	Nematodes/semi-persistent	ELISA, RT-PCR	Yes	No	Yes	Yes	Yes	Yes
Strawberry leaf curl	StLCV	*Begomovirus*	Whiteflies/semi-persistent	ELISA, PCR	N/A	N/A	N/A	Yes	N/A	N/A
Strawberry mild yellow edge	SMYEV	*Potexvirus*	Aphids/persistent	ELISA. RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Strawberry mottle	SMoV	*Sadwavirus*	Aphids/Semi-persistent	RT-PCR	Yes	Yes	Yes	N/A	Yes	Yes
Strawberry necrotic shock	SNSV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR	Yes	N/A	Yes	N/A	Yes	Yes
Strawberry pallidosis	SPaV	*Crinivirus*	Whiteflies/semi-persistent	RT-PCR	Yes	Yes	N/A	N/A	N/A	Yes
Strawberry pseudo mild yellow edge	SPMYEV	*Carlavirus*	Aphids/ nonpersistent	ELISA?	Yes	N/A	N/A	N/A	Yes	N/A
Strawberry vein banding	SVBV	*Caulimovirus*	Aphids/semi-persistent	PCR	Yes	Yes	Yes	Yes	Yes	Yes

Tobacco necrosis D	TNVD	*Necrovirus*	Olpidium/?	ELISA/RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Tobacco streak virus	TSV	*Ilarvirus*	Pollen/seed[d]	ELISA, RT-PCR	Yes	Yes	Yes[e]	Yes	Yes	Yes[e]
Tomato black ring	TBRV	*Nepovirus*	Nematodes/semi-persistent	ELISA, RT-PCR	No	N/A	Yes	N/A	Yes	N/A
Tomato ringspot	ToRSV	*Nepovirus*	Nematodes/semi-persistent	ELISA/RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes

[a]Indicative of conventional and qRT-PCR.
[b]Pollen and seed transmitted.
[c]Also transmitted by pollen-feeding arthropods.
[d]Not confirmed in *Fragaria* X *ananassa*.
[e]May have been an isolate of SNSV.

Table 2 List of viruses known to infect raspberry, blackberry, and their hybrids worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Apple mosaic	ApMV	*Ilarvirus*	Pollen/seed[a]	ELISA, RT-PCR[b]	Yes	Yes	Yes	Yes	Yes	Yes
Arabis mosaic	ArMV	*Nepovirus*	Nematodes/semi-persistent[c,d]	ELISA, RT-PCR	Yes[e]	Yes[e]	Yes	Yes[e]	Yes[e]	Yes[e]
Beet pseudo-yellows	BPYV	*Crinivirus*	Whiteflies/semi-persistent	ELISA, RT-PCR	Yes	Yes[e]	Yes[e]	Yes[e]	Yes[e]	Yes[e]
Blackberry chlorotic ringspot	BCRV	*Ilarvirus*	Pollen/seed	RT-PCR	Yes	N/A	Yes	N/A	Yes	N/A
Blackberry vein banding	BVBaV	*Ampelovirus*	Mealybugs/semi-persistent?	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blackberry virus E	BVE	*Unassigned*	Unknown (eriophyid mites?)	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blackberry virus S	BVS	*Marafivirus*	Unknown (leafhoppers?)	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blackberry virus Y	BVY	*Brambyvirus*	Unknown (eriophyid mites?)	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blackberry yellow vein	BYVaV	*Crinivirus*	Whiteflies/semi-persistent	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A

Black raspberry necrosis	BRNV	*Sadwavirus*	Aphids/ nonpersistent	RT-PCR	Yes	N/A	Yes	N/A	N/A	N/A
Cherry leaf roll	CLRV	*Nepovirus*	Pollen/seed (nematodes?)[a]	ELISA, RT-PCR	Yes	Yes[e]	Yes	N/A	Yes[e]	Yes
Cherry rasp leaf	CRLV	*Cheravirus*	Pollen/seed (nematodes?)	ELISA, RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Grapevine Syrah Virus 1	GSyV-1	*Marafivirus*	Unknown (leafhoppers?)	RT-PCR	Yes	Yes[e]	N/A	N/A	N/A	N/A
Impatiens necrotic spot	INSV	*Tospovirus*	Thrips/persistent	ELISA, RT-PCR	Yes	Yes[e]	Yes[e]	Yes[e]	Yes[e]	Yes[e]
Raspberry bushy dwarf	RBDV	*Ideovirus*	Pollen/seed	ELISA, RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Raspberry latent	RpLV	*Unassigned*	Aphids/persistent	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Raspberry leaf curl	RLCV	*Unknown*	Unknown	Grafting	Yes	N/A	N/A	N/A	N/A	N/A
Raspberry leaf mottle	RLMV	*Closterovirus*	Aphids/semi-persistent	RT-PCR	Yes	N/A	Yes	N/A	N/A	N/A
Raspberry leaf blotch	RLBV	*Emaravirus*	Unknown (eriophyid mites?)	RT-PCR	N/A	N/A	Yes	N/A	N/A	N/A
Raspberry vein chlorosis	RVCV	*Rhabdovirus*	Aphids?	RT-PCR	Yes?	N/A	Yes	N/A	N/A	Yes
Raspberry ringspot	RpRSV	*Nepovirus*	Aphids/semi-persistent	ELISA, RT-PCR	No	No	Yes	N/A	Yes	No

Continued

Table 2 List of viruses known to infect raspberry, blackberry, and their hybrids worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale—cont'd

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Rubus canadensis 1	RuCV-1	Unassigned	Unknown	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Rubus yellow net	RYNV	*Badnavirus*	Aphids/semi-persistent	PCR	Yes	N/A	Yes	N/A	N/A	N/A
Sowbane mosaic	SoMV	*Sobemovirus*	Pollen/seed	ELISA, RT-PCR	Yes	Yes[e]	Yes	Yes[e]	Yes[e]	Yes[e]
Strawberry latent ringspot	SLRSV	Unassigned	Nematodes/semi-persistent	ELISA, RT-PCR	Yes[e]	No	Yes	Yes[e]	Yes[e]	Yes[e]
Strawberry necrotic shock	SNSV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR	Yes	N/A	Yes?	N/A	Yes?	Yes?
Tomato black ring	TBRV	*Nepovirus*	Nematodes/semi-persistent[d]	ELISA, RT-PCR	No	N/A	Yes	N/A	Yes[e]	N/A
Tomato ringspot	ToRSV	*Nepovirus*	Nematodes/semi-persistent[d]	ELISA/RT-PCR	Yes	Yes[e]	Yes[e]	Yes[e]	Yes[e]	Yes[e]
Tobacco ringspot	TRSV	*Nepovirus*	Nematodes/semi-persistent	ELISA/RT-PCR	Yes	Yes[e]	Yes[e]	Yes[e]	Yes[e]	Yes[e]
Wineberry latent/ Blackberry calico	WLV/BlCV	Unassigned	Unknown		Yes	N/A	Yes	N/A	N/A	N/A
Blackberry leaf mottle	BLMaV	*Emaravirus*	Eriophyid mites?	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A

[a]Not confirmed in *Rubus*.
[b]Indicative of conventional and qRT-PCR.
[c]Pollen and seed transmitted.
[d]Also transmitted by pollen-feeding arthropods.
[e]Present but not reported in Rubus species.

Table 3 List of viruses known to infect blueberry and cranberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Blueberry shock	BlShV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR[a]	Yes	N/A	N/A	N/A	N/A	N/A
Blueberry latent	BlLV	*Amalgavirus*	Unknown	RT-PCR	Yes	N/A	N/A	N/A	Yes	N/A
Blueberry latent spherical	BLSV	*Nepovirus*	Nematodes/semi-persistent[b,c]/?	RT-PCR	N/A	N/A	N/A	N/A	Yes	N/A
Blueberry leaf mottle	BLMoV	*Nepovirus*	Nematodes/semi-persistent?[b,c]	ELISA, RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blueberry mosaic	BlMV	*Ophiovirus*	Olpidium/?	RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes
Blueberry necrotic ring blotch	BNLBV	Unassigned	Unknown	RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Blueberry red ringspot	BRRV	*Soymovirus*	Unknown	ELISA/PCR	Yes	N/A	Yes	N/A	Yes	Yes
Blueberry scorch	BlScV	*Carlavirus*	Aphids/nonpersistent	ELISA, RT-PCR	Yes	N/A	Yes	N/A	N/A	N/A
Blueberry shoestring	BlSSV	*Sobemovirus*	Aphids/nonpersistent	ELISA, RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A

Continued

Table 3 List of viruses known to infect blueberry and cranberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale—cont'd

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Blueberry virus A	BVA	*Closterovirus*	Aphids/semi-persistent?	RT-PCR	Yes	N/A	N/A	N/A	Yes	Yes
Cherry leaf roll	CLRV	*Nepovirus*	Pollen/seed (nematodes?)	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes[d]	N/A	Yes[d]	Yes
Peach rosette mosaic	PRMV	*Nepovirus*	Nematodes/semi-persistent[b,c]	ELISA, RT-PCR	Yes	N/A	Yes[d]	N/A	Yes[d]	N/A
Strawberry latent ringspot	SLRSV	Unassigned	Nematodes/semi-persistent[b,c]	ELISA, RT-PCR	Yes[d]	No	Yes[d]	Yes[d]	Yes[d]	Yes
Tobacco ringspot	TRSV	*Nepovirus*	Nematodes/semi-persistent[b,c]	ELISA/RT-PCR	Yes	Yes[d]	Yes[d]	Yes[d]	Yes[d]	Yes[d]
Tobacco streak	TSV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR	Yes	Yes[d]	Yes[d]	Yes[d]	Yes[d]	Yes[d]
Tomato ringspot	ToRSV	*Nepovirus*	Nematodes/semi-persistent[b,c]	ELISA/RT-PCR	Yes	Yes	Yes[d]	Yes[d]	Yes[d]	Yes[d]

[a]Indicative of conventional and qRT-PCR.
[b]Pollen and seed transmitted.
[c]Also transmitted by pollen-feeding arthropods.
[d]Present but not in blueberry or cranberry.

Table 4 List of viruses known to infect currant and gooseberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Cucumber mosaic	CMV	*Cucumovirus*	Aphids/nonpersistent	ELISA, RT-PCR[a]	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Alfalfa mosaic	AlMV	*Alfamovirus*	Aphids/nonpersistent	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Arabis mosaic	ArMV	*Nepovirus*	Nematodes/semi-persistent[b,c]	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Black currant reversion	BRV	Nepovirus	Eriophyid mites/semi-persistent	ELISA, RT-PCR	No	N/A	Yes	N/A	Yes	Yes
Blackcurrant leafroll 1	BCLRaV-1	*Closterovirus*	Aphids/semi-persistent?	RT-PCR	N/A	N/A	Yes	N/A	N/A	N/A
Gooseberry vein banding	GVBaV	Badnavirus	Seed/pollen/aphids/semi-persistent	PCR	Yes	N/A	Yes	N/A	N/A	N/A
Raspberry ringspot	RpRSV	*Nepovirus*	Nematodes/semi-persistent	ELISA, RT-PCR	No	No	Yes	N/A	Yes[d]	No
Sowbane mosaic	SoMV	*Sobemovirus*	Pollen/seed	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Strawberry latent ringspot	SLRSV	Unassigned	Nematodes/semi-persistent	ELISA, RT-PCR	Yes[d]	No	Yes	Yes[d]	Yes[d]	Yes[d]

Continued

Table 4 List of viruses known to infect currant and gooseberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale—cont'd

					Regional occurrence					
Virus name	**Acronym**	**Genus**	**Transmission**	**Laboratory detection**	**NA**	**SA**	**Europe**	**Africa**	**Asia**	**Australia/ NZ**
Tobacco rattle	TRV	*Tobravirus*	Nematodes/semi-persistent	ELISA/ RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Tomato ringspot	ToRSV	*Nepovirus*	Nematodes/semi-persistent	ELISA/ RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]

[a]Indicative of conventional and qRT-PCR
[b]Pollen and seed transmitted.
[c]Also transmitted by pollen-feeding arthropods.
[d]Not confirmed in Ribes.

Table 5 List of viruses known to infect elderberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale

Virus name	Acronym	Genus	Transmission	Laboratory detection	Regional occurrence					
					NA	SA	Europe	Africa	Asia	Australia/NZ
Apple mosaic	ApMV	*Ilarvirus*	Pollen/seed	ELISA, RT-PCR[a]	Yes	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Arabis mosaic	ArMV	*Nepovirus*	Nematodes/ semi-persistent[b,c]	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Blueberry scorch	BlScV	*Carlavirus*	Aphids/ nonpersistent	ELISA, RT-PCR	Yes[d]	N/A	Yes	N/A	N/A	N/A
Cherry leaf roll	CLRV	*Nepovirus*	Pollen/seed (nematodes?)	ELISA, RT-PCR	Yes[d]	Yes[d]	Yes	N/A	Yes[d]	Yes[d]
Cucumber mosaic	CMV	*Cucumovirus*	Aphids/ nonpersistent	ELISA, RT-PCR	Yes	Yes[d]	Yes	Yes[d]	Yes[d]	Yes[d]
Elderberry carlaviruses	ECVs	*Carlavirus*	Aphids/ nonpersistent?	RT-PCR	Yes	N/A	Yes	N/A	N/A	N/A
Elderberry latent	ELV	Carmovirus	Soil/pollen/seed	ELISA, RT-PCR	Yes	N/A	N/A	N/A	N/A	N/A
Strawberry latent ringspot	SLRSV	Unassigned	Nematodes/ semi-persistent	ELISA, RT-PCR	Yes[d]	No	Yes	Yes[d]	Yes[d]	Yes[d]
Tobacco ringspot	TRSV	*Nepovirus*	Nematodes/ semi-persistent	ELISA/ RT-PCR	Yes	Yes[d]	Yes[d]	Yes[d]	Yes[d]	Yes[d]

Continued

Table 5 List of viruses known to infect elderberry worldwide, including acronym, genus, means of transmission, laboratory tests available for detection, and occurrence of each virus on a continental scale—cont'd

Virus name	Acronym	Genus	Transmission	Laboratory detection	Regional occurrence					
					NA	SA	Europe	Africa	Asia	Australia/NZ
Tomato black ring	TBRV	*Nepovirus*	Nematodes/ semi-persistent	ELISA, RT-PCR	No	N/A	Yes	N/A	Yes	N/A
Tomato bushy stunt	TBSV	Tombusvirus	Soil/pollen/seed	ELISA, RT-PCR	Yes	Yes	Yes	Yes	Yes	No
Tomato ringspot	ToRSV	*Nepovirus*	Nematodes/ semi-persistent	ELISA/ RT-PCR	Yes	Yes	Yes	Yes	Yes	Yes

[a]Indicative of conventional and qRT-PCR.
[b]Pollen and seed transmitted.
[c]Also transmitted by pollen-feeding arthropods.
[d]Not confirmed in elderberry.

potted and acclimated in screenhouses with very minimal exposure to virus vectors. In most certification standards, plants are not allowed to flower or fruit in nurseries, to minimize the risk of infection by pollen-borne viruses. Thus, somewhere in the plant multiplication process, plants need to evaluated for trueness-to-type to ensure that an off-type was not propagated, this is true for conventional or tissue culture propagated nursery stock. In the United States, this is the responsibility of the nursery, not the Clean Plant Centers.

A golden rule for nursery production of berry crops, or for any crop, is to locate nurseries so that they are isolated from production fields of the same crop. As mentioned above, production fields are managed to control disease rather than controlling viruses. Therefore, if located nearby to a production field, nurseries could be under extreme virus pressure based on vectors in the area. This juxtaposition of nurseries and production fields, likely contributed to the high level of virus infection in nursery stock in strawberry in eastern Canada in 2012 (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013).

There are generally two to three cycles of propagation in nurseries, and each successive stage should require less stringent testing, thus, a G2 block would require more testing than a G3 block, and a G3 block would require more testing than a G4 block. G2 material is propagated to produce G3 material, and then G3 material is propagated to produce G4 material, which is sold to fruit growers. Therefore, an infection at the G2 level will result in its multiplication in the nursery system as well as provide a source of inoculum for further spread within the nursery. This is the rationale for having more stringent testing at the G2 level than G3, etc. There is debate whether the final stage of propagation in the nursery should be subjected to visual inspection or if there should be some level of testing. It is our contention that there should be a level of testing for the one or two highest risk viruses in the region. Based on hypergeometric sampling strategies, only 59 plants need to be tested to provide a 95% confidence that there is less than a 5% infection rate in the block (Anonymous, 2008). We would suggest that serological tests (ELISA) be developed for these high-risk or "canary" viruses to keep the cost of testing low, but effective. This level of testing will ensure that there has not been a complete breakdown in the system such as occurred recently in strawberry nurseries in Canada and California. As was shown in those cases, visual inspection was not adequate to detect the problem, which only became obvious once the plants were transplanted in fruit growers fields, and millions of dollars of crop were lost (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Martin & Tzanetakis, 2013).

The BMPs are based on the ecology and biology of the vectors of viruses that occur in the region, and are often defined in a certification standard. An explanation of why requirements are in the standard in terms of the vectors and the virus–vector relationships helps the nursery managers to appreciate the importance of following the BMPs, rather than just viewing them as arbitrary dictates from government regulators. For nematode-vectored viruses, cropping history, site selection, preplant nematode testing, and preplant soil treatment are addressed in the certification standard. Cropping history information is related to potential survival of viruses with nematode or fungal vectors. Therefore, the cropping history information often inquires about crops that can serve as hosts for these viruses and vectors rather than being limited to history of the nursery crop that is planned for the site. This is especially true for many of the nematode-transmitted viruses, which have fairly broad host ranges and thus, the potential to remain viable at a site for many years. As an example, a research plot used for *Tomato ringspot virus* research in strawberry in the 1980s had viable virus at the site in 2013 even though strawberries had not been grown at the site in more than 30 years (Martin, personnel observation). The virus has a broad host range and can perennate at a site for many years by infecting a range of broad leaf weeds, etc., or in this case, raspberries had also been grown at the site off and on during the 30 years. There are multiple methods to eliminate or greatly reduce nematode populations, including the use of soil fumigation and fallowing. Fallowing requires the absence of any plants that can serve as hosts for the nematode. Eliminating virus from a site can be accomplished in several ways in addition to soil fumigation, fallowing the location, or planting with a nonhost for the virus can be very effective (Pinkerton & Martin, 2005). The latter did not eliminate nematodes from the site, but virus control was equivalent to that obtained with fumigation with methyl bromide.

For aphid-transmitted viruses, isolation distances listed in a certification standard will be dependent on the type of virus/vector interaction and efficiency of aphid transmission, i.e., nonpersistent viruses will have a shorter isolation distance than persistently transmitted viruses that can be carried a long distance by the aphid vector. Another important consideration is host range of the aphid and virus, for example, the strawberry aphid has a very limited host range that includes *Fragaria* spp., *Potentilla* spp., and very occasionally Rosa spp. (Forbes & Chan, 1989), thus isolation from these hosts is critical rather than from all vegetation. Additionally, the four most important aphid-transmitted viruses of strawberry (Strawberry crinkle, Strawberry mild yellow edge, Strawberry mottle, and Strawberry veinbanding viruses)

have limited host ranges and have only been reported in *Fragaria* spp. in nature, making most non-*Fragaria* vegetation near a nursery very low risk as virus reservoirs for these viruses. In blueberry, *Blueberry scorch virus* is transmitted very inefficiently (Lowery et al., 2008) where groups of 25 aphids only transmitted the virus to about 20% of the test plants using the most efficient of 8 aphid species tested. Additionally, this virus is transmitted in a non-persistent manner suggesting a relatively short isolation distance could greatly reduce the risk from this virus to nursery plants. In several cases, ilarviruses have been shown to be transmitted by thrips, thus if ilarviruses are present in the area of a nursery thrips transmission should be considered.

In most cases, pollen transmitted viruses should be of little concern to nursery planting stock, if the nursery plants are not allowed to flower. In the case of *Blueberry shock virus*, the horizontal transmission in field settings can be very rapid depending on genotype, thus even few flowers in a nursery setting could provide a conduit for transmission, if there are infected field or native plants nearby. Recent, work with *Raspberry bushy dwarf virus* (RBDV) demonstrated the ability of cross-family transmission via pollen through stigma infection, even though the pollen tube did not completely penetrate the stigma (Isogai, Yoshida, Nakanowatari, & Yoshikawa, 2014). This is likely a very rare event that would pose very little risk in a nursery setting with limited flowering of the plants. It may explain a mechanism for host jumping of viruses that are limited to pollen transmission.

Recently, several eriophyid mite-transmitted viruses, or viruses where the best guess vector is an eriophyid mite based on sequence analysis, have been identified in berry crops (Hassan et al., 2013; McGavin et al., 2012; Quito-Avila, Brannen, Cline, Harmon, & Martin, 2013). These vectors are extremely small and screening would not prevent them from entering a screenhouse or screened greenhouse. Thus, in areas where these viruses are present along with the vectors, production of nursery stock free of these viruses will be very difficult. Thrips-transmitted viruses pose a similar risk in that thrips-proof screening greatly limits any airflow and in warmer environments it would be very difficult to prevent extreme heat buildup in screenhouses. In such cases, it would be necessary to develop a pest management program to control the eriophyid mites and/or thrips.

8. BMPS, KNOWING THE HIGH-RISK VIRUSES

There are more than 80 viruses reported to infect berry crops (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Martin & Tzanetakis,

2006; Martin, Polashock, & Tzanetakis, 2012), but fortunately in any given area the number of viruses that need to be managed is much smaller. A key to managing viruses in nursery settings is to know what are the high-risk viruses in the region and where the nursery is located (Martin & Tzanetakis, 2013). As an example, for *Rubus* nurseries in the Pacific Northwest there are four viruses of concern given that site selection and preparation have addressed the issue with nematode-transmitted viruses. These viruses include *Black raspberry necrosis virus* (Secoviridae, unassigned genus), *Raspberry leaf mottle virus* (Closterovirus), *Raspberry latent virus* (Reoviridae, unassigned genus), and *Rubus yellow net virus* (Badnavirus), all of which are transmitted by the large raspberry aphid, *Amphorophora agathonica* (Converse, Stace-Smith, & Jones, 1987). Thus, controlling a single vector should be the main focus in managing these viruses. In addition, studies on flights of this vector have shown that it is not moving early in the season (approximately 950 days, base 50 from Jan 1), in northern Washington flights of this aphid start mid to late June, with a sharp peak through mid-July then very little aphid movement until late in the season (Lightle, Quito-Avila, Martin, & Lee, 2014). This suggests that vector control can be targeted, with most efforts aimed at the peak flight times. Additionally, for certifying agencies, monitoring of virus infection in *Rubus* nurseries in this region should focus on these four viruses for floricane type *Rubus* cultivars, since they do not flower in the first year canes that would be present in nurseries. For primocane fruiting cultivars, it will be necessary to consider the pollen-borne viruses: RBDV, *Strawberry necrotic shock virus*, *Apple mosaic virus*, and *Blackberry chlorotic ringspot virus*, since these cultivars flower in first year canes and will very likely have flowers in the nursery mid to late in the summer (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013).

9. VIRUS CONTROL IN COMMERCIAL FIELDS

Fruit growers are interested in disease control rather than virus control, which is fortunate since many of the viruses of berry crops are symptomless (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Martin et al., 2012; Martin & Tzanetakis, 2013) or produce symptoms but have a very minor impact on crop production when present in single infections (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013). *Blackberry calico virus* produces dramatic symptoms but has minimal impact on yield or quality (Converse, 1987), it spreads rapidly and thus control in a grower's field could not be justified. In many parts of the world, strawberry production is

done with annual plantings, which means that if plants from the nursery are free of, or have a very low incidence of virus infection, growers can produce a profitable crop with little costs for virus control. In perennial strawberry production, vector control is often required. The other berry crops are all grown as longer term perennials and in the case of blueberries it may take 3–5 years after planting before the first crop is harvested, thus, vector control can be very important depending on vector populations and transmission efficiency. *Blueberry shoestring virus* in areas where there is an efficient vector and virus inoculum present is an example of a case where vector control is necessary to manage this disease in the field (Ramsdell, 1987).

9.1. Virus Resistance and Tolerance

There are few examples of virus resistance in berry crops, the best known and most widely used is resistance to RBDV, which is controlled by a single dominant gene. This source of resistance is used widely in breeding programs but appears to be closely linked with some negative horticultural traits, since breeders have had difficulty developing acceptable cultivars with RBDV resistance. A resistance breaking strain of RBDV (RBDV-RB) has been reported in Europe and Russia (Wilson, Knight, & Barbara, 1983) but has not been detected in other parts of world. RBDV-RB infects almost all raspberry cultivars that have been reported to be resistant to the virus (Knight & Barbara, 1999). The fact that there are cultivars that are resistant to the RBDV-RB strain suggests that there are multiple genes for resistance to RBDV that could be pyramided for a more durable resistance. In blueberry, "Bluecrop" is resistant to *Tomato ringspot virus* and can be used in areas where the virus and nematode vector are present. Since blueberry is a long-term crop, ideally >20 years, soil fumigation to control nematodes is not very effective since nematodes below the fumigant control profile in the soil will migrate up and infect plants before they are in full production.

Virus tolerance is very common in the cultivars of strawberry, raspberry, and blackberry. In these crops, very few viruses other than the nepoviruses cause symptoms in single infections. In some cases, such as "Totem" or "Puget Reliance" strawberries, plants are tolerant to mixed infections with *Strawberry veinbanding*, *Strawberry mottle*, and *Strawberry mild yellow edge viruses*. Prior to 2000, this tolerance had been very useful for production in Oregon, Washington, and British Columbia where aphid populations are very high most years, since these were the three common aphid-borne viruses in this region. Starting about 2000, the incidence of SCV increased rapidly in this

area, and since then the virus tolerance has been much less effective. In annual strawberry production, the plants are in the fruiting fields for less than a year; thus if starting with "clean" plants, virus diseases often are not a problem since very few plants will have a disease causing complex at the end of the production cycle (Martin & Tzanetakis, 2013). In areas where the strawberry aphid (*Chaetosiphon* spp.) does not occur, viruses should be a minor problem for strawberry production. The four viruses that cause most damage in strawberry worldwide are transmitted by aphids in this genus, and if these viruses are not present the whitefly-transmitted criniviruses are asymptomatic. Raspberry mosaic disease is caused by a virus complex where many cultivars are tolerant to any single component of the complex, but mixed infections can lead to a serious disease (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013). The same is true with blackberry yellow vein disease, which can be caused by a number of different virus combinations, and the more viruses the more serious the disease (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013). For fruit growers, virus tolerance is a very important component in disease management.

When vector management is necessary, growers can target specific virus vectors to control part of a virus complex rather than trying to control all viruses. Identifying which vector to target should be based on the vector biology, i.e., is it dispersing throughout the growing season (whiteflies)? Is it a sedentary feeder most of the season as is the case with many aphids? In the case of the aphid-borne viruses in red raspberry, aphid flights occur over a short time period during the season (Lightle et al., 2014) making control easier than for many other types of aerial vectors. Thus, control measures should focus on the easiest vector(s) to manage to achieve disease control, rather than trying to control all vectors. A potential problem with tolerant cultivars is that they can serve as a source of inoculum that can spread to adjacent cultivars that lack virus tolerance.

9.2. Vector Resistance

Aphid resistance has been deployed very successfully in red raspberry that has resulted in resistance to the raspberry mosaic disease complex (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013). In North America, a single dominant gene has been used for over 40 years and provided high levels of resistance. In the last decade, there have been biotypes of the large raspberry aphid that has overcome this resistance (Dossett & Kempler, 2012). Aphid resistance to the European large raspberry aphid (*Amphorophora idaei*)

has been less successful. Multiple dominant genes for resistance to this aphid have been deployed, Ag_1 from red raspberry and Ag_{10} from black raspberry, as well as several minor genes for resistance, and in all cases new biotypes of the aphid developed that overcame the resistance. Recently, aphid resistance has been identified in native populations of *Rubus occidentalis* from several locations in North America (Dossett & Finn, 2010), and the mechanism of the aphid resistance in black raspberry is different from that in red raspberry (Lightle, 2013). This suggests that it should be possible to pyramid the two types of aphid resistance to develop a more durable resistance that can be used to protect raspberries against aphid-borne viruses. It is not known if the mechanism of resistance from the Ag_{10} gene that came from black raspberry is the same as that of the resistance gene identified in black raspberry more recently in North America.

There are two sources of resistance to the blackcurrant gall mite (*Cecidophyopsis ribis*) that have been used successfully for mite control, which is a serious pest of black currants and also vectors BRV (Jones, Brennan, McGavin, & Lemmetty, 1998), the most damaging virus of blackcurrants. One gene, *P*, is from *Ribes nigrum* ssp. *sibiricum* (Anderson, 1971), and the second, *Ce* (Knight, Keep, Briggs, & Parker, 1974) is derived from gooseberry. These genes are used widely in black currant breeding programs, and efforts are underway using molecular markers to pyramid these genes to develop more durable resistance (Mazeikiene, Bendokas, Stanys, & Siksnianas, 2012).

9.3. High-risk Viruses and Mixed Infections

Effective virus disease control in fruit production fields requires knowledge of the viruses that are present and spreading in the area, which of these viruses lead to disease when they occur in mixed infections. These are the high-risk viruses for the area. How each of the high-risk viruses is vectored is also important in developing a virus disease control program. When the risk of virus disease is evaluated, cultivar selection should consider any vector resistance and virus resistance or tolerance that is available. In the Pacific Northwest, the four aphid-transmitted viruses are the high-risk strawberry viruses. In this region, virus disease control in strawberry cultivars that have tolerance to multiple aphid-transmitted viruses but exhibit disease when infected with three or four of the aphid-vectored viruses can be accomplished with vector control that targets the weakest links in the disease complex. In this case, SCV is the easiest virus to target since has a long latent

period in the vector, is only transmitted by *Chaetoshipon* spp., and this aphid has a relatively narrow window of dispersal during the growing season (Sylvester, Richardson, & Frazier, 1974). Thus, one to three well-timed sprays during peak aphid flights can be quite effective at controlling this virus, and as a result virus disease in cultivars with tolerance to multiple aphid-vectored viruses.

In blackberries in the southeastern United States, there are several virus complexes that cause blackberry yellow vein disease, with a different complex observed in Arkansas, Mississippi, and North Carolina (Martin, MacFarlane, et al., 2013; Martin, Peres, et al., 2013; Susaimuthu, Tzanetakis, Gergerich, Kim, et al., 2008; Susaimuthu, Tzanetakis, Gergerich, & Martin, 2008; Thekke-Veetil et al., 2013). This disease is more complicated to control since within each complex there are multiple vectors that transmit viruses (Poudel, Ho, Laney, Khadgi and Tzanetakis, 2014; Poudel et al., 2013). However, the same principle applies: know the viruses in the area that contribute to the disease, know their vectors, and when they disperse and develop control measures based on the easiest virus(es) to control given the biology of the vector and virus/vector interactions. In all berry crops other than strawberry, the plantings are expected to be fruitful for 10 years or more. With these crops, there is a longer period of time for plantings to come into production, so replanting is much more expensive in terms of lost production. Thus, virus control is more critical since the plants need to be protected for multiple growing seasons before they are productive.

9.4. Coordinated Control Efforts

In some situations, the primary virus inoculum in a region is from the crop itself rather than from native vegetation. This is the case for the aphid-borne viruses in strawberry in production areas where there are few native strawberries. Even if there are native strawberries, the production fields are often the most important source of virus inoculum. In areas where strawberries are grown as perennials, with a cropping cycle of 3–4 years, the aphid-borne viruses are primarily circulating between the production fields. This is the case in the Pacific Northwest of the North America (Oregon, Washington, and British Columbia). Effective virus control in these situations is best achieved through a coordinated vector control program for a full cropping cycle. Thus, implementation of an area-wide aphid management program for 4 years to reduce the aphid and virus pressure in the area will greatly reduce virus inoculum. In this case, the viruses and vector are primarily

limited to *Fragaria* species. Without a coordinated effort, the vectors and viruses will continue to rotate between fields and a high level of vector and virus pressure will be a never ending problem.

Controlling whitefly-transmitted viruses in strawberry in California is much more challenging than controlling the aphid-borne viruses, since the whitefly (*Trialeurodes vaporariorum*) has a broad host range and is an active flyer throughout the season (Tzanetakis, Martin, & Wintermantel, 2013; Wintermantel, 2004). Additionally, one of the criniviruses in strawberry (*Beet pseudo yellows virus*) has a broad host range and the strawberry production in many parts of California occurs in areas with very diverse agriculture. In this case, the best strategy is to focus efforts on the aphid-transmitted viruses simply because the vector and viruses are primarily limited to strawberry hosts. Additionally, in tests with mixed infections of the whitefly-transmitted criniviruses in strawberry there were not observed disease symptoms in the absence of any aphid-borne viruses in several cultivars tested including "Hood" one of the most sensitive strawberry cultivars in terms of virus disease.

Isolation from other production fields of the same crop is very effective at limiting virus disease pressure if one starts with "clean" plants. In the absence of virus, vector populations often are not a problem. If vector populations reach levels to be a pest problem in the absence of virus, control often only needs to be targeted to reduce populations at harvest time to minimize contaminants in the harvested fruit. In some cases, vectors can reach populations to become serious pests for crop production, and control is required regardless of the presence of virus. However, in most cases economic thresholds for vector control are much lower if managing for virus control than they are if managing for vector control in the absence of virus. As an example, strawberry fields located on Lulu Island along the coast in British Columbia had no virus symptoms after 4 years even though the vector populations were quite high. There is only one strawberry grower on the island, and the air currents are coming from Pacific Ocean. This was at the same time, when strawberry fields 40 km inland from Lulu Island were experiencing severe virus problems (Martin, unpublished). Isolation from other commercial fields can be very effective in control of pollen-borne viruses.

Effective control of virus diseases in berry crops is dependent on knowledge of the viruses, vectors, the virus/vector relationship, their distribution geographically, vector phenology, host resistance and tolerance to viruses and/or vectors. As researchers, we are trained to focus on the diseases and their management, but growers also need to consider all factors in growing, harvesting, and marketing their crops. In many cases, what we consider

optimal disease management strategies may not fit well into fruit production systems. Labor availability may be more critical for when a specific management practice is implemented then when an aphid flight is occurs. The marketability of a specific cultivar may be much more important than whether it is virus or vector resistant. As researchers and extension specialists, we provide information to growers, but must realize that they need to consider the entire fruit production enterprise rather than just disease control to remain profitable. Understanding the constraints that fruit growers have to deal with will help us develop control measures that can better serve the industries.

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