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A century of plant virus management in the Salinas Valley of California, 'East of Eden'

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Abstract

The mild climate of the Salinas Valley, CA lends itself well to a diverse agricultural industry. However, the diversity of weeds, crops and insect and fungal vectors also provide favorable conditions for plant virus disease development. This paper considers the incidence and management of several plant viruses that have caused serious epidemics and been significant in the agricultural development of the Salinas Valley during the 20th century. *Beet curly top virus* (BCTV) almost destroyed the newly established sugarbeet industry soon after its establishment in the 1870s. A combination of resistant varieties, cultural management of beet crops to provide early plant emergence and development, and a highly coordinated beet leafhopper vector scouting and spray programme have achieved adequate control of BCTV. These programmes were first developed by the USDA and still operate. *Lettuce mosaic virus* was first recognized as causing a serious disease of lettuce crops in the 1930s. The virus is still a threat but it is controlled by a lettuce-free period in December and a seed certification programme that allows only seed lots with less than one infected seed in 30 000 to be grown. 'Virus Yellows' is a term used to describe a complex of yellows inducing viruses which affect mainly sugarbeet and lettuce. These viruses include *Beet yellows virus* and *Beet western yellows virus*. During the 1950s, the complex caused significant yield losses to susceptible crops in the Salinas Valley. A beet-free period was introduced and is still used for control. The fungus-borne rhizomania disease of sugarbeet caused by *Beet necrotic yellow vein virus* was first detected in Salinas Valley in 1983. Assumed to have been introduced from Europe, this virus has now become widespread in California wherever beets are grown and crop losses can be as high as 100%. Movement of infested soil and beets accounts for its spread throughout the beet-growing regions of the United States. Control of rhizomania involves several cultural practices, but the use of resistant varieties is the most effective and is necessary where soils are infested. Rhizomania-resistant varieties are now available that perform almost as well as the non-resistant varieties under non-rhizomania conditions. Another soil-borne disease termed lettuce dieback, caused by a tomato bushy stunt-like tombusvirus, has become economically limiting to romaine and leaf lettuce varieties. The virus has no known vector and it seems to be moved through infested soil and water. Heavy rains in the past 4 years have caused flooding of the Salinas River and lettuce fields along the river have been affected severely by dieback. Studies are now in progress to characterize this new virus and identify sources of resistance. Agriculture in the Salinas Valley continues to grow and diversify, driven by demands for 'clean', high quality food by the American public and for export. The major aspects of plant virus control, including crop-free periods, breeding for resistance, elimination of inoculum sources, and vector control will continue to be vital to this expansion.

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Undoubtedly, the advances in crop production through genetic manipulation and advances in pest management through biological control will eventually become an important part of agricultural improvement.

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1. Introduction

“The Salinas Valley is in Northern California. It is a long narrow swale between two ranges of mountains, and the Salinas River winds and twists up the center until it falls at last into Monterey Bay, …, .On the wide level acres of the valley the topsoil lay deep and fertile. The spring flowers in a wet year were unbelievable. The whole valley floor, and the foothills too, would be carpeted with lupins and poppies.” (John Steinbeck, ‘East of Eden’, 1952).

The booming agricultural community has changed the appearance of the Salinas Valley in Monterey county of California since the days of Steinbeck. The climate of cool summers and mild winters together with the unique fertile soils facilitate the continuous cultivation of many crops in overlapping sequence. This area is suitable particularly for cool-season fruits and vegetables including lettuce, broccoli, celery, spinach, cauliflower, strawberries, grapes, artichokes, asparagus, and many other specialty crops. Until recently, sugarbeet was also a major crop in Salinas Valley. However, economics and diseases, in particular rhizomania, have severely limited beet production. The value of Monterey county’s agriculture was a record $2.3 billion in 1998. Between April and October, the Salinas Valley supplies $\sim$80% of the lettuce marketed in the US. Because of the importance of the Salinas Valley to vegetable production, in particular lettuce, it is often referred to as the ‘salad bowl’ of America.

The diversity of weeds, crops, and insect and fungal vectors in the Salinas Valley provide favourable conditions for plant virus disease development and several viral diseases have caused serious epidemics in crops since the early 1900s. Management of these diseases has been based primarily on crop-free periods, classically-derived host-plant resistance, eradication of inoculum sources and weed control. Some of the diseases encountered continue to cause problems in beet and vegetable production, not only in Salinas Valley, but also in other agricultural areas of California and elsewhere in the US. This paper considers some of the most important viral diseases that have threatened agriculture in the Salinas Valley since the early 1900s and their effective management.

2. *Beet curly top virus* (BCTV)

The California sugarbeet industry was established in the 1870s. Soon afterward a disease, referred to as ‘curly top,’ began to be recognized throughout the western US. (Bennett, 1971). This disease spread quickly and soon virtually destroyed the newly established industry (Fig. 1). Long before curly top was shown to be caused by BCTV (family, *Geminiviridae*; genus, *Curtovirus*), control measures were adopted that are still used. Breeding for resistance began in 1918 when the USDA and the Spreckles Sugar Company in Salinas hired Dr Katherine Esau to investigate resistance to BCTV. In 1929, US Congress appropriated funds for studies on curly top and the beet leafhopper vector (*Circulifer tenellus* (Baker)). The first curly top-resistant sugarbeet variety was released in 1933. In 1947, the USDA established a permanent research laboratory in Salinas to work on pathology, entomology and breeding for BCTV control.

Prior to the agricultural development of the western US, natural vegetation did not support large populations of the beet leafhopper (BLH). However, as land use changed to intermittent farming and overgrazing by livestock occurred, the stable plant cover of perennial grasses and shrubs (primarily sagebrush; *Artemisia tridentata* Nutt.) was replaced by winter and summer annuals (Carter, 1930). The preferred environment of the BLH is that of a desert. Preferred hosts of BLH that succeeded the original plant cover included mustards (*Brassica* spp.), Russian thistle (*Salsola kali* L., var. *tenuifolia* Tausch.), filaree [*Erodium cicutarium* (L.)L'Her.], and *Plantago* sp. L. on which the vector thrived and attained plague proportions (Piemeisel et al., 1951). The BLH transmits BCTV from weeds to beet, bean, melon, and tomato, causing large economic losses. To control the BLH, an extensive spray programme was started in 1943 and directed at the breeding grounds. That year the programme cost $350 000, and DDT was used to spray 4–40 ha three or four times. The programme now costs $1.3 million, and involves the insecticide malathion.

Control of the BLH is only one of several measures used against BCTV. Breeding programmes for resistance or tolerance to the virus have produced some valuable material, but resistance is less effective when young beet plants are exposed to large population of viruliferous BLH. Timing of planting to promote rapid early growth is critical for sugarbeet. In the early stages of crop growth, cultivars considered to be highly tolerant or resistant are still susceptible to infestation by the BLH and infection with BCTV. As the beets

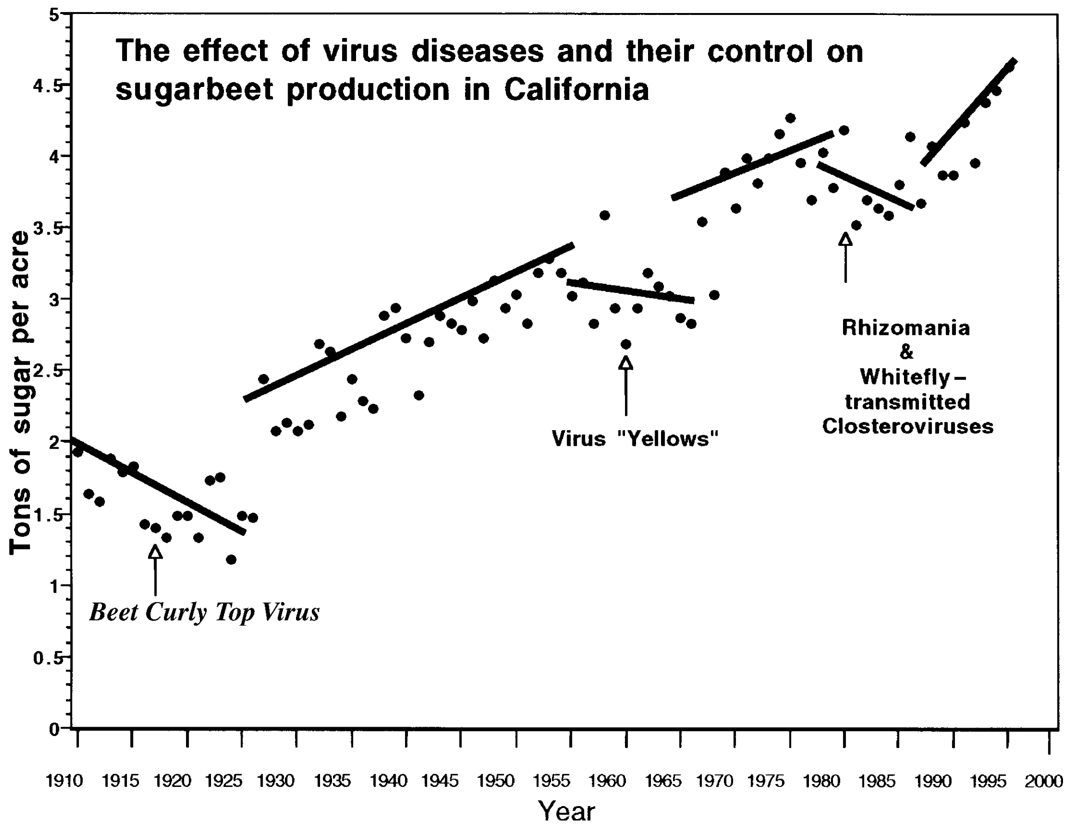

Fig. 1. Production of sugar per acre from sugarbeet in California, 1911–1999. A combination of host-plant resistance, crop-free periods, weed control, elimination of sources of inoculum and vector control have achieved the effective management of viral diseases in sugarbeet.

grow and shade the soil, they become less susceptible to infestation. Although resistant varieties are available, they are not always grown. Farmers' choice of variety is a complex process based on local climate, sugar yield, insect populations, and local disease pressures, i.e., rhizomania, *Cercospora* leafspot, and rots caused by *Erwinia* spp., *Phytophthora* spp., and *Pythium* spp. A goal of sugarbeet breeders is to combine high levels of curly top resistance with resistance to other diseases and with high yield characteristics.

A study was made in Idaho to reseed extensive leafhopper breeding areas with native grasses and shrubs on which BLH does not reproduce. This was based on the concept of 'replacement control, which employs an indirect means of getting rid of pests through changes in vegetation' (Piemeisel and Carsner, 1951). Between 1959 and 1972 over 100 000 ha (77% of the total wild host area) were reseeded with crested wheatgrass (*Agropyron cristatum*), on which BLH does not reproduce. Unfortunately, thorough evaluations were not made, but general assessments indicated that the BLH populations were greatly reduced and curly top was no longer severe in either vegetables or sugarbeet. Losses to sugarbeet were reduced by over $1 million annually and livestock production was increased a similar amount on reseeded land (Knipling, 1979).

The current control measure of applying malathion to thousands of hectares in the state of California is threatened by the increasing restrictions on the use of insecticides registered for application to crops and weeds. At a recent curly top board meeting, it was stated that "beet leafhoppers don't cross barbed-wire fences". For example, a livestock farmer who manages land effectively by allowing grasses and shrubs to be maintained has low BLH populations, whereas a neighbour directly alongside, who allows livestock to eat vegetation to the ground, has a carpet of broadleaf plants conducive to BLH. This should be an indication that the 'replacement control' approach described by Piemeisel in 1954 should be adopted for curly top control in the future. Economics and pesticide use policy are likely to determine which management procedures will be used.

3. *Lettuce mosaic virus* (LMV)

Lettuce mosaic virus (LMV) (family, *Potyviridae*; genus, *Potyvirus*) was an important limiting factor in lettuce production in the Salinas Valley from the 1930s to the 1960s. Whether alone or together with other viruses (e.g. *Beet western yellows*, *Lettuce speckles*, *Beet yellow stunt*, *Tomato spotted wilt*, or *Sowthistle yellow vein*), LMV caused significant economic losses. Early studies by Newhall (1923) in California, and by Kassanis (1947), Broadbent (1951) in England confirmed that LMV was seed-borne, but also established that phytosanitation and crop isolation were important for successful crop production. Grogan et al. (1952) tested the control of LMV through virus-free seed. Zink et al. (1956) later showed that the percentage of plants that become infected in the field largely depends upon the amount of seed-borne virus and the numbers and mobility of the aphid vectors. For example, if 0.1% or more of seed is infected, control is likely to be unsatisfactory. After evaluation of all the epidemiological evidence, the following control methods were devised, (i), use of seed lots in which no infected seed in 30 000 was detected; (ii), removal of weeds adjacent to lettuce plots; (iii), removal of lettuce residues after harvest; and (iv), a lettuce-free period of several weeks before planting. These measures are still used in lettuce growing areas of California and elsewhere. The continued production of lettuce depends on the strict adherence of these practices to avoid LMV epidemics.

4. Virus yellows

The term 'virus yellows' is commonly used in the sugarbeet industry to describe a complex of yellows-inducing viruses that are aphid-transmitted. This complex consists of *Beet western yellows virus* (family, *Luteoviridae*; genus, *Polerovirus*), beet chlorosis virus (BChV; a proposed member of the *Luteoviridae*) (Liu et al., 1999), and *Beet yellows virus* (BYV; family, *Closteroviridae*; genus, *Closterovirus*). *Beet mosaic virus* (BtMV; family, *Potyviridae*; genus, *Potyvirus*) is often part of this complex, but its role in the yellowing disease is uncertain. In Europe, *Beet mild yellowing virus* (family, *Luteoviridae*; genus, *Polerovirus*) is also considered to be a part of the virus yellows complex. Early descriptions suggest that virus yellows occurred in the Salinas Valley as early as 1921 (Bennett, 1960). Factors influencing the epidemiology of the disease include vector populations, virus–vector relationships and virus sources.

The two most important viruses involved in the yellowing complex are BYV and BWYV. BYV is transmitted in a semi-persistent manner and is retained by the vector for less than 72 h. This type of transmission indicates that spread of the virus from the source is localized, i.e. the disease incidence is high in areas adjacent to the virus source but rapidly decreases with distance (Duffus, 1983). The primary source of BYV is beet itself, including overwintering crops and 'volunteer' plants in abandoned fields or waste sites. *Beet western yellows virus* (BWYV) is transmitted in a persistent manner by aphids. Thus, distribution of BWYV is more general and widespread than that of BYV. BWYV also infects numerous weeds and other crops, including lettuce (Duffus, 1973).

After curly top resistance was first introduced in 1934, beet yields continued to increase due to improvements in the cultivars available, increased use of nitrogen fertilizers, improved stand establishment, irrigation methods, insect and nematode control. Yields were further enhanced by the introduction of hybrid and monogerm seed. However, from 1950 until the late 1960s beet yields declined progressively because of an increased incidence of virus yellows. This disease was also referred to as 'June Yellows' in the Salinas Valley because by mid-summer, beet, spinach and lettuce fields were often completely yellow.

Epidemiological studies in the late 1950s (Duffus, 1963) established a close correlation between virus yellows incidence and the proximity of overwintered beet fields. Sugarbeet growers and processors reached agreements to maintain beet-free periods between harvesting and sowing new crops throughout California. These include the destruction of volunteers or 'groundkeepers' and weed beets. Beet-free periods differ between beet growing districts because of the diverse planting dates throughout the state due to the different climates. These programmes were first introduced for the 1968 crop. Following the introduction of beet-free periods in 1968, the mean sugar yields in California increased by approximately 40% for the subsequent growing seasons (Fig. 1).

Since 1985, virus yellows has recurred in northern California due to increased aphid populations and the decreased effectiveness of beet-free periods. The green peach aphid *Myzus persicae* was formerly the most common aphid vector of the yellows virus complex. In recent years, however, populations of the black bean aphid, *Aphis fabae*, have increased. Although it is a less efficient vector than *M. persicae*, *A. fabae* has complicated the exploitation of beet-free periods as a means of disease management because it is more heat tolerant than *M. persicae* and has longer flight periods which extends the period of time during which aphid transmission occurs. Thus, beet-free periods are now even more important than previously and the beet industry has enforced them within beet production districts.

5. Rhizomania of sugarbeet

Rhizomania was first reported in the US in Paso Robles, California, approximately 80 miles south of Salinas Valley in 1984 (Duffus et al., 1984). However, rhizomania symptoms were observed in Salinas Valley beet fields at least one year before the first official report. Rhizomania, or 'crazy root' refers to the excessive hairy root proliferation that results from infection by the *Beet necrotic yellow vein virus* (BNYVV; genus, *Benyvirus*). This virus has a rigid, rod-shaped morphology and is transmitted by the soil-borne plasmodiophorid-like fungus, *Polymyxa betae* Keskin (Richards and Tamada, 1992; Tamada et al., 1975). Once introduced to a site, rhizomania is thought to persist almost indefinitely in infested soils.

At the time rhizomania was introduced, only a few virus-tolerant beet varieties were available from Europe, and none was adapted to Californian conditions due to susceptibility to other pathogens. Breeding programmes for resistance were initiated at that time and continue on the rhizomania-infested fields at the USDA-ARS in Salinas (Lewellen and Biancardi, 1990; Lewellen et al., 1987).

In the 1960s, Monterey county produced approximately 16 000 ha of beets. Over the years, the area has steadily declined due to several factors, including a shift to vegetable and grape production, the enforced withdrawal of Telone as a soil fumigant to control rhizomania and sugarbeet cyst nematode (*Heterodera schachtii* Schmidt), and the high cost of the energy required to irrigate fields and transport harvested roots. Rhizomania has also been a significant factor limiting beet production in Monterey county and throughout California. In 1997, the last commercial beet crop was planted and amounted to only a few hundred hectares. California produced approximately 25% of sugar in the US during the 1970s and 1980s. That figure is now down to approximately 10% (Sugar and Sweetener Situation and Outlook Reports, 1971–1998). Rhizomania is currently widespread throughout California wherever beets are grown, and was probably spread widely long before the disease was recognized. In other beet growing states, strict regulations are in place to limit the spread or introduction of rhizomania.

Several factors are important in the management of rhizomania including planting into cool soils, proper irrigation, and soil fumigation where this is allowed. However, host-plant resistance is the most critical aspect of rhizomania control. Breeding programmes for rhizomania resistance have developed some valuable germplasm, and current varieties have resistance genes that originated from sugarbeet and from the wild beet relative, *Beta maritima* L. (*B. vulgaris* spp. *maritima* L.) (Lewellen and Biancardi, 1990). Until recently, sugarbeet growers were reluctant to plant rhizomania-resistant varieties because they typically yielded less than susceptible beets where rhizomania was absent. Currently, rhizomania-resistant varieties perform under high rhizomania pressure (in areas including the San Joaquin Valley of California) almost as well as susceptible varieties in the absence of rhizomania. Breeding programmes in Salinas Valley rely heavily on evaluations of the severity of rhizomania symptoms based on the international scale adopted for sugarbeet germplasm. Root weight and sucrose content are also measured routinely and used to evaluate rhizomania resistance. Recently, a study was done on infested fields in Salinas where TAS-ELISA values were compared with the biological evaluations across eight sugarbeet cultivars that ranged in resistance to rhizomania from uniformly susceptible to resistant. Differences in absorbance at A_{405nm} correlated closely with the dosage and frequency of the *Rz* resistance allele which conditions resistance to BNYVV. For example, a diploid (*Rzrz*) hybrid had a significantly lower absorbance value than a similar triploid (*Rzrzrz*) hybrid. In addition, the absorbance values were positively correlated with the rhizomania disease index score, and negatively correlated with individual root weight, plot root weight, and sugar yield (Fig. 2) (Wisler et al., 1999). For all cultivars, absorbance values decreased as the growing season progressed. This information is extremely important for the sugarbeet industry when considering cultivar choices, optimum time for assaying by ELISA, inoculum production in soils and future crop rotations.

Economic constraints that are independent of virus problems may limit the future of sugarbeet production in the Salinas Valley. The problem of resistance to rhizomania has been solved; however, beets cannot compete with the lucrative vegetable and fruit crops that are now being grown. In order to maintain beet production in California, the possibility of other soil-borne diseases should be addressed. There are other soil-borne *Polymyxa*-transmitted viruses of sugarbeet that have not yet been detected in California, but occur in other beet-growing states (Wisler et al., 1994). It is likely that these viruses may eventually reach California. The beet industry is now evaluating the threat posed by these viruses and will be testing new sources of resistance.

6. Lettuce dieback

A previously uncharacterized dieback disease of lettuce has been observed throughout the Salinas Valley, Santa Maria, and Orange counties, Cali-

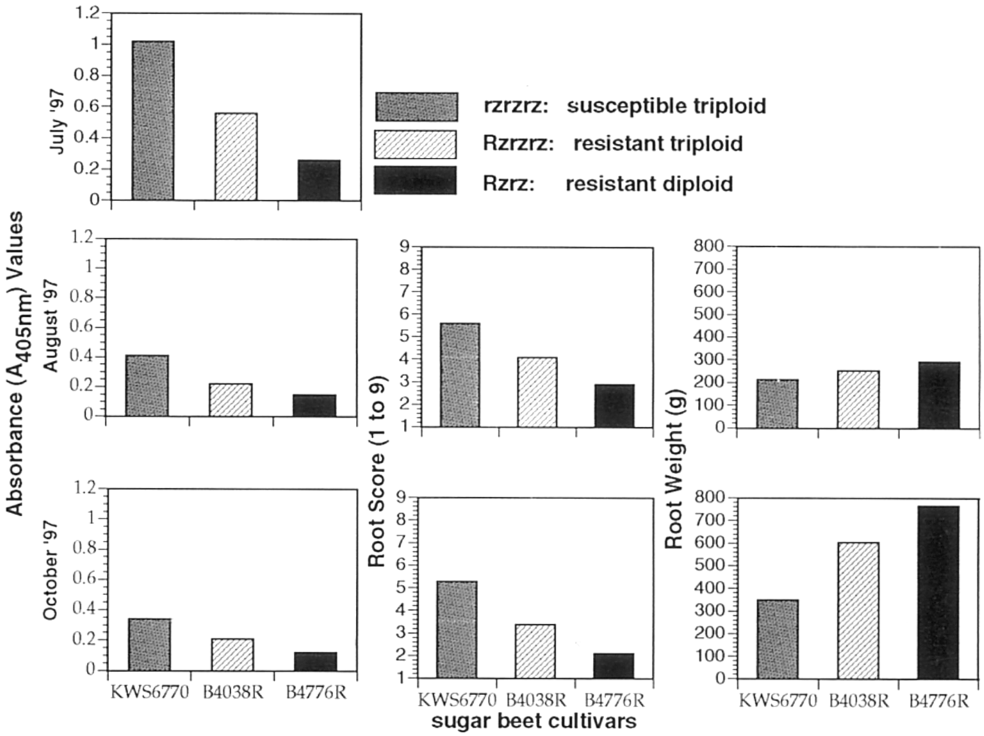

Fig. 2. Three cultivars which range from uniformly susceptible (*rzrzrz*; KWS6770), to diploid resistant (*Rzrz*; Beta4776R), to triploid resistant (*Rzrzrz*; Beta4038R) for BNYVV were chosen to illustrate the association between dosage of the *Rz* allele and three variables which were measured in this study, including absorbance in TAS-ELISA for BNYVV at A_{405nm}, rhizomania root score and root weight. A highly positive correlation was observed between allelic dosage and absorbance values for BNYVV for the three harvest dates. For the last two harvest dates, a positive correlation was observed between allelic dosage and root score, whereas a highly negative correlation was observed between allelic dosage and root weight.

fornia and in Yuma, AZ since 1994. Symptoms of this disease are unlike those of other known fungal, bacterial or viral diseases of lettuce. Attempts to isolate a causal fungal or bacterial pathogen consistently failed. Symptoms include yellowing, necrosis, stunting and dieback of affected plants. The disease primarily affects romaine and leaf lettuce types, which have increased significantly in area cultivated in the late 1990s. Several isolates of *Tomato bushy stunt virus* (TBSV; family, *Tombusviridae*; genus, *Tombusvirus*) have been recovered from symptomatic romaine lettuce as well as from leaf lettuces and one crisphead lettuce variety from the Salinas Valley. Dieback is causing increased concern to growers and some have encountered 60% or more crop loss. The disease has been found primarily in low-lying areas near rivers, in areas where soil has been dredged from a drainage area and spread onto the field, or in flooded locations. Heavy rains and flooding of farmland in recent years and a shift in the lettuce varieties planted from primarily crisphead to 30% leafy types has contributed to the increasing incidence of lettuce dieback which is primarily associated with fields along the Salinas River.

A syndrome of unknown cause referred to as ‘brown blight’ in the mid-1920s was possibly caused by a virus similar to the TBSV recently isolated, and was extremely destructive on the crisphead variety ‘New York’, which was the predominant variety planted at the time throughout California (Jagger, 1939). A resistant variety, ‘Imperial’, was selected from ‘New York’ and essentially replaced the former crisphead type. In varietal trials to find resistance in romaine and leaf lettuce types during the 1998 and 1999 growing seasons, both 'New York' and 'Imperial' were planted, and showed the same reaction to the current lettuce dieback as they did to 'brown blight' in the early 1900s. All 21 romaine varieties, one of the four green leaf varieties, and all four of the red leaf varieties were susceptible to this disease. In a recent trial, three resistant romaine plant introductions (PIs) were found with characteristics that are almost suitable for commercial production. It is not known yet if methyl bromide fumigation will be effective for control, but with the impending ban on the compound this approach may not be a feasible, long-term plan for disease management.

Diagnostic assays including western blot analyses and immunocapture-RT-PCR have been tested for virus detection directly from lettuce. Due to low concentration of TBSV in infected plants, the virus must be inoculated to sensitive indicator plants before using these tests in order to identify the virus reliably. In all assays, TBSV or viruses closely related to it have been isolated from symptomatic lettuce. The 3′-terminal gene (P19) of the viral genome for each isolate has been increased by RT-PCR and their sequences have been determined. The results of such analyses show that a wide range of TBSV isolates and possibly even distinct tombusviruses cause lettuce dieback. Some isolates are sufficiently similar in sequence homology (96%) to TBSV to be considered as isolates of the same virus. Two isolates differ sufficiently (84–86%) from TBSV to be considered as new strains, or even as distinct tombusviruses (Obermeier et al., 1999). Two isolates were chosen for pathogenicity studies and were shown to be the causal agent of the disease by pouring and recirculating inoculum from infected *Nicotiana clevelandii* test plants into soil planted with lettuce.

Regardless of whether lettuce dieback is caused by a unique tombusvirus isolate or several related ones, control of this soil-borne virus disease, which has no known natural vector, is best accomplished by using resistant lettuce cultivars. TBSV is an extremely stable virus and it is likely to survive in soil and water for long periods of time. The use of soil fumigants in the Salinas Valley is common, especially for strawberries, but adds considerable expense and may be limited in the future. Fortunately, three PI lettuce lines have already been identified that are resistant to lettuce dieback and show promise for future breeding efforts to develop resistant romaine and leaf lettuces.

7. Conclusions

The unique environment of the Salinas Valley, CA provides many examples of damaging plant viruses and the need for effective control. Celery mosaic virus is controlled by celery-free periods. *Tomato spotted wilt virus* (family, *Bunyaviridae*; genus, *Tospovirus*) is rarely a problem because of the excellent weed control practiced in this intensive agricultural area. Whitefly-transmitted viruses are uncommon because the climate limits the development of whitefly populations except in greenhouses. *Tomato infectious chlorosis virus* (TICV; family, *Closteroviridae*; genus, *Crinivirus*), which is transmitted by the greenhouse whitefly (*Trialeurodes vaporariorum*), has been found in local greenhouses infecting tomato, lettuce, petunia, and ranunculus. *Beet pseudoyellows virus* (BPYV; family, *Closteroviridae*; genus, *Closterovirus*) has also been detected in greenhouse-grown cucurbits and ornamentals. Whitefly control and a knowledge of the persistence of criniviruses in whiteflies is crucial. For example, TICV persists in the vector for 3–4 days, whereas BPYV persists for 9 days. This information is important for the management of greenhouse crops. The management practices that have been most successful for control of plant viruses include crop-free periods, vector control, elimination of inoculum sources, weed control, and use of virus-resistant varieties. This has come through the collaboration of the agricultural industry, pathologists, geneticists, and entomologists. In future, the agricultural industry of the Salinas Valley is expected to grow and diversify. Additional disease control measures are likely to include genetically-engineered resistance to viruses and various forms of biological control. It is to be hoped that agriculturists will have the foresight to protect the unique environment so that it continues to be available for productive farming using environmentally sound management practices.

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