CHAPTER 1

APPEARANCE AND EXPANSION OF TYLCV: A HISTORICAL POINT OF VIEW

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1. INTRODUCTION

In 1959, the Israeli Ministry of Agriculture urged farmers in the Jordan Valley to replace the tasty but soft tomato "Marmande" with the long–shelf life variety "Money Maker," which was more suitable for export. A month after transplanting (August), most of the tomato plants in the region were affected by a disease of unknown etiology. Symptoms included severe stunting of plant growth, erect shoots, and markedly smaller and misshaped leaflets. The leaflets that appeared immediately after infection were cupped down and inward, and subsequently developing leaves were strikingly chlorotic and showed an upward curling of the leaflet margins. When young plants were infected, they barely produced any marketable fruits (Cohen & Nitzany, 1960). The growers' first reaction was to blame the change in tomato variety and they demanded compensation from the Ministry of Agriculture. Dr. F. E. Nitzany, head of the Virology Laboratory at the Volcani Center, Agricultural Research Organization (ARO), Israel, was asked to determine the causal agent of the disease and find solutions to the problem. A field survey revealed that most of the tomato plots in the area had been completely destroyed, and that the disease was accompanied by large populations of whiteflies. The whitefly population had built up in the nearby cotton fields, a crop which was being grown on a commercial scale for the first time in Israel. Soon enough, the suspicion that the whiteflies were the vector of the disease was confirmed, following controlled transmission experiments in the laboratory. Moreover, the "Marmande" tomato was found to be as susceptible as "Money Maker" to the disease, which was found to be viral in nature (Cohen & Nitzany, 1960). The virus was named *Tomato yellow leaf curl virus* (TYLCV) by the late Professor I. Harpaz of the Hebrew University (Cohen & Harpaz, 1964). Interestingly, similar disease symptoms had first been

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observed on tomatoes grown in the Jordan Valley as early as 1929, as well as in subsequent years (Avidov, 1944). The outbreaks of TYLCV disease were always accompanied by large populations of whiteflies (Cohen & Berlinger, 1986). However, the geminate shape of the viral capsid was first observed in 1980 (Russo et al., 1980), and it was only in 1988 that the virus was isolated (Czosnek et al., 1988). It took another 3 years to clone and sequence the virus, and to demonstrate that the genome of TYLCV is composed of only one single-stranded (ss) DNA molecule (Navot et al., 1991).

The first evidence of economic damage to vegetable crops caused by the whitefly *Bemisia tabaci* (Gennadius) in Israel was recorded in 1931 (Avidov, 1944). Since 1935, it has been a permanent pest, mainly in the Jordan Valley. Avidov concluded that the *Bemisia* whitefly can raise as many as 15 generations per year in the Jordan Valley, due to the favorable climate in the area (Avidov, 1944). The silvering of squashes caused by *Bemisia*, which was observed as early as 1963 (Baery & Kapoller, 1963), and the very wide host range of this insect indicate that the B (or silverleaf) biotype has been present in this region for a long time.

2. VIRUS–VECTOR INTERACTIONS

2.1. Acquisition and transmission

In 1960, the first steps were taken toward controlling the TYLCV epidemic. The virus–vector relationship was studied by testing the transmission efficiency of TYLCV by whiteflies. Following 48 h of acquisition access feeding on infected tomato, only 5% of the male whiteflies transmitted the virus by transmission feeding of a single insect per test plant. However, female whiteflies were able to transmit the virus with 32% efficiency, sixfold better than their male counterparts. Transmission feeding with 1, 3, 5, 10, and 15 viruliferous female whiteflies per plant yielded transmission rates of 32%, 83%, 84%, 86%, and 100%, respectively (Cohen & Nitzany, 1966).

It was found that the virus is circulative and persistent in the insect (Cohen & Nitzany, 1966). Once the whitefly vector feeds on an infected host plant and acquires the virus, viral transmission can occur within hours, and may continue for the life span of the vector. Acquisition and transmission thresholds were found to be between 15 and 30 min. However, at least 4 h were required to obtain high infection rates. The latent period was found to be from 21 to 24 h. In tests carried out with whiteflies having a life span of 20–50 days, following 48 h of acquisition feeding, only 2 out of 39 female whiteflies retained the virus for 20 days. Shorter acquisition feedings resulted in shorter virus-retention periods. TYLCV transmission efficiency by its vector declines with time; most of the females failed to transmit the virus for more than 10 days after acquisition (Cohen & Nitzany, 1966). Besides acquisition by adults, it was found that the virus is also acquired by the whitefly larval stages. Following feeding on an

infected plant, 28% of the emerging adults were able to transmit the virus (Cohen & Nitzany, 1966).

To test for virus transmission from viruliferous females to their progeny (transovarial transmission), viruliferous whiteflies were allowed to lay eggs on cotton plants, which are immune to TYLCV. Upon emergence from the pupal stage, the adult offspring were immediately transferred to TYLCV-susceptible plants for a 48 h transmission feeding. Out of 360 female offspring tested, none was found to transmit the virus. Thus it was concluded that TYLCV is not transmitted to the whitefly progeny.

The issue of whether TYLCV is transmitted transovarially to the whitefly progeny came up again for debate 30 years later, when different findings were published. Using molecular tools as well as PCR amplification (which were unavailable back in the 1960s), it was demonstrated that TYLCV DNA is transmitted transovarially to the progeny of viruliferous whiteflies (Ghanim et al., 1998). This was confirmed in an independent study by Polston et al. (2001) who also found that progeny of viruliferous whiteflies indeed contain TYLCV DNA. In another study, Bosco et al. (2004) demonstrated that DNA of *Tomato yellow leaf curl Sardinia virus* (TYLCSV) is transmitted to the whitefly progeny, whereas DNA of TYLCV is not. However, while according to one study (Ghanim et al., 1998), the TYLCV-carrying whitefly progeny were able to transmit the virus to test plants, in other studies (Polston et al., 2001; Bosco et al., 2004), the whitefly progeny, although containing TYLCV DNA, were unable to transmit the virus, supporting the original results obtained in the late 1960s (Cohen & Nitzany, 1966).

2.2. Periodic acquisition

While studying virus–vector interactions, a unique phenomenon, which was termed "periodic acquisition," was observed (Cohen & Harpaz, 1964). It was found that following TYLCV acquisition, viruliferous whiteflies progressively lose infectivity and about 10 days after completion of the acquisition feeding period, most of the insects are no longer able to transmit the virus. However, during that period, the vector is unable to compensate for its steadily decreasing viral-transmission capacity by reacquiring the virus from the infected source plant. That is, another cycle of acquisition feeding, while the vector can still transmit the virus (albeit at a decreasing efficiency), does not restore the transmission capability to its original efficiency. The vector must first completely lose its transmission ability before it can reacquire the virus (Cohen & Harpaz, 1964). A proteinaceous factor which appeared to be related to the phenomenon was found in homogenates of insects, and was termed periodic acquisition-related factor (PARF). This factor, via membrane feeding to nonviruliferous whiteflies, inhibited acquisition, transmission, and retention of TYLCV by the whiteflies (Cohen, 1967, 1969; Marco et al., 1972). Unfortunately, research into the mechanism underlying this phenomenon was never completed. Therefore,

whether this is an active antiviral mechanism or a temporary blockage of the salivary glands by degradation products of the viral capsid protein remains a mystery.

The long latent period of 21 h, the phenomenon of periodic acquisition, and the relatively long and efficient inoculation period of about 4 h suggest that the use of a fast-killing insecticide could effectively control the spread of TYLCV. Indeed, soon after the epidemics broke out, it was demonstrated that spraying with the cyclodiane "Andrin" solved the problem (Cohen et al., 1963). However, the whiteflies soon developed resistance to the insecticide and research shifted to cultural crop management and sanitation.

3. THE USE OF YELLOW MULCH TO PROTECT CROPS

In 1940, while working in the Jordan Valley, a researcher named K. M. Mendel observed that mulching of summer tomato nurseries with sawdust accelerates seedling growth (Avidov, 1944). This growth acceleration was attributed to the finding that the soil temperature under the mulch was cooler by 8–10°C than the temperature of bare soil. However, it was also noticed that the whitefly population on the mulched seedlings was much lower than on nonmulched seedlings (Avidov, 1944). Avidov first thought that the smell of the resin secreted from the sawdust repelled the insects. However, the same controlling effect was achieved by mulching the seedlings with straw and the scent-effect theory was rejected. Avidov also found that during the day, the temperature immediately above the sawdust mulch sometimes reached 47–51°C (temperatures that were later found to be lethal to whiteflies in a dry climate). He therefore concluded that the repelling effect of the sawdust mulch occurs by creating "an atmosphere of death" on its surface which repels the whiteflies (Avidov, 1944).

In an attempt to better understand the effect of straw mulching on whiteflies, the possible effect of whitewashing seedbed soil on whiteflies was also studied (Avidov, 1944). It was found that, 8 days after sprouting, the average number of whitefly eggs per seedling for whitewashed soil was 18.5, compared to 60 whitefly eggs per seedling in nonmulched soil. The same maximum soil surface temperature was recorded for the whitewashed soil (44°C) and the nonmulched control plot (45°C). These findings suggested that soil surface temperature is not the only factor involved in the mulch-based whitefly-controlling mechanism (Avidov, 1944).

3.1. How does it work?

Following Avidov's observations, Nitzany et al. (1964) demonstrated that, indeed, straw mulch can reduce the spread of another whitefly-borne virus, the semipersistent *Cucumber vein yellowing virus* (CVYV). Mulching cucumber seedlings with straw markedly reduced the whitefly population and, as a consequence, delayed CVYV spread for about 10 days. The straw mulch also increased

yield and vegetative development of the cucumber plants (Nitzany et al., 1964). Subsequent to Nitzany's work from 1964, straw mulch was used to control the spread of TYLCV (Cohen et al., 1974). The mulch was very effective in preventing the spread of the virus and the whitefly populations for the first 18 days following germination. However, it was important to extend the duration of the mulch's controlling effect beyond the first 18 days after germination, and the described putative mechanism underlying this effect was therefore reevaluated. In 1962, Mound demonstrated that yellow color attracts whiteflies (Mound, 1962). It was suggested that yellow radiation, which induces vegetative behavior, may be a component of the insect host–selection mechanism (Mound, 1962). This raised the possibility that yellow color also contributes to the controlling effect of the mulch. Thus, using an aphid flight chamber, the effect of straw on whitefly dispersal was studied (Cohen et al., 1974). It was found that nearly three times more whiteflies were attracted to sticky cardboard plates covered with straw compared to those covered with tomato leaves. Moreover, the number of whiteflies attracted to fresh straw was double the number of whiteflies attracted to old straw which had first been exposed to field conditions for 25 days (Cohen et al., 1974). It should be noted that the yellow color of fresh straw is much more intense than that of old straw, the latter fading with exposure to intense solar radiation.

The correlation between the mulch controlling effect and its attractiveness to whiteflies was demonstrated by testing the effects of four different-colored mulches on whiteflies: straw, and three different-colored polyethylene sheets – yellow, silver, and blue (Cohen & Melamed-Madjar, 1978). All four mulches reduced the spread of TYLCV compared to the nonmulched control, with the yellow mulch being the most effective. Moreover, the yellow mulch was the most attractive to whiteflies, in both an aphid flight chamber and the field. In the latter experiments, sticky traps consisting of Petri dishes covered with different-colored polyethylene sheets or with cropped straw were used. The traps were placed on same-colored mulch treatments. Indeed, 77 whiteflies were trapped on the yellow mulch, while only 39 whiteflies (nearly half) were trapped on the silver mulch, 23 whiteflies were trapped on the blue mulch, and 11 whiteflies were trapped on the straw mulch (Cohen & Melamed-Madjar, 1978). Once again, these results clearly demonstrated that the whiteflies were attracted to the yellow color of the mulch.

3.2. Effect of temperature

To study the role of temperature in the controlling ability of the yellow mulch the following experiments were carried out. Four temperature-controlled heating plates (each 10 cm in diameter) were attached to the floor of a flight chamber, 20 cm apart (Cohen, 1982). Yellow-painted Petri dishes covered with glue on the upper side were placed on the heating plates. The temperature of two opposing plates was set to 25°C, and that of the other two to 50°C. In each

experiment, 200 whiteflies were introduced into the flight chamber from the top; the number of insects adhering to the traps was counted 1 h later. After seven repeats, no significant differences were found in the attraction of the whiteflies to yellow traps heated to 50°C (total of 559 whiteflies) or to 25°C (total of 538 whiteflies) (Cohen, 1982). This indicated that high temperature does not repel the whiteflies, as it had been previously suggested (Avidov, 1944).

In another experiment, the combined effect of color and heat was studied. A similar experimental design was used except that, in this case, the yellow traps were not covered with glue, so the attracted whiteflies that landed on the traps could then fly away. The number of dead whiteflies found on each yellow trap was recorded 1 h after their release into the chamber. This time, the results showed significant differences between the treatments; significantly more dead whiteflies were found in the high-temperature plates. Thus, following a total of seven different experiments, no dead whiteflies were found on the plates heated to 25°C, compared with 203 dead whiteflies found on the plates heated to 35°C (Cohen, 1982). These results also contradicted the earlier hypothesis that whiteflies are repelled by high temperature. The controlling effect of yellow mulch therefore appears to be due to a combination of the whitefly attraction to the yellow color of the mulch and its consequent death due to dehydration induced by the high temperature of the mulch. It should be noted that the typical Israeli climate is semiarid – high temperature and low humidity. Moreover, in the tomato-growing regions, soil temperatures exceeding 30°C are quite common. Thus, the use of yellow plastic mulch to protect vegetable crops from whiteflies and whitefly-borne viruses has become common practice in Israeli agriculture (Zaks, 1997).

4. TYLCV EPIDEMIOLOGY

4.1. Wild hosts

In a series of studies aimed at finding ways to control viral spread, a search for the virus inoculum sources in the hot valleys of Israel was performed (Cohen et al., 1988). The surveys were carried out by collecting seeds or cuttings of plants and weeds (mainly the perennials) common to the Jordan Valley region. The samples (seedlings or cuttings) were inoculated with TYLCV to determine which species is susceptible to the virus and which could serve as a potential host. Plants that were found to be susceptible to the virus were tested again for the presence of TYLCV in another set of samples brought from the field. *Cynanchum acutum* was found to be the only natural perennial host of TYLCV. This weed is concentrated along the western bank of the Jordan River (where it covers large areas), a few kilometers east of the main tomato production region at the time. During the winter months (December–February), only the subterranean parts of the plant survive. The plants start growing again in the spring, reaching full vegetation in August–September, concomitant with the

increase in the whitefly population and the tomato-transplanting period. Since this host was concentrated at some distance from the tomato-growing areas, it was important to determine whether whiteflies could cross this distance. Therefore, an area of about 100 m^2, fully covered with *C. acutum* plants and a large population of whiteflies, was dusted with "Fire Orange," a daylight-fluorescent dust, using a mechanical hand duster (Cohen et al., 1988). This dust persisted on the whiteflies for at least 9 days. Whitefly movement was recorded by positioning yellow sticky traps at various distances from the dusted plants, and these traps were monitored weekly for the appearance of fluorescent whiteflies. Indeed, 1 week after the release, fluorescent whiteflies were found in the tomato fields, at a distance of 7 km from the dusting site.

4.2. Viruliferous whiteflies

Most interesting results were obtained when the percentage of viruliferous whiteflies in the general whitefly population was studied during the peak population period (September–November in our case), at which time the infection rate of nonprotected tomato plants reaches 90–100% (Cohen et al., 1988). Whiteflies were collected in the field from different hosts using a cordless rechargeable vacuum cleaner adapted to collect insects into a plastic cylinder (Cohen et al., 1989). The insects were released into a cage with a glass top and were then collected in groups of 20 into small clip cages. The clip cages were placed on the leaves of healthy tomato test plants (one clip cage per plant) and the whiteflies were allowed to feed for 48 h. Following this inoculation access period (IAP), the clip cages were removed, and the test plants were sprayed and monitored for the development of disease symptoms. Only 5.4% of the whitefly population collected on *C. acutum* was viruliferous, compared with 3.2% of the whiteflies collected from a tomato field. One explanation for the relatively low percentage of viruliferous whiteflies within this field population may be the aforementioned periodic acquisition effect.

4.3. Crop-free period

The Arava region of Israel is a 200 km long, 5–10 km wide arid region extending from the Dead Sea to the Red Sea. The climatic conditions during the winter, and moderate temperatures combined with intense solar radiation due to lack of clouds, make this region ideal for growing vegetable crops. The lack of water in the region is overcome by a pipeline from the north and the use of local wells. In 1982–1986, severe viral epidemics occurred in the Arava, threatening the future of vegetable crop cultivation in the region. The major viruses were found to be *Zucchini yellow mosaic virus* (ZYMV) and *Cucumber mosaic virus* (CMV) in cucurbits, *Potato virus Y* (PVY) in pepper, and TYLCV in tomato.

In Israel, TYLCV is widespread mainly in the late summer and autumn, due to the peaking whitefly population during that period (September–November).

The tomato season in the Arava region begins in mid-August. At that time, no infected wild hosts of TYLCV, such as the annual *Malva parviflora* or the perennial *C. acutum*, are found in the region. To determine whether the virus is already present at the beginning of the tomato season in the Arava region, tomato trap plants were distributed in the fields of the Arava and left for a week. Then the plants were collected, sprayed, and kept in an insect-proof greenhouse where the appearance of TYLCV-induced symptoms was monitored. No virus was found in the tomato trap plants dispersed weekly from June to the beginning of the tomato season in August. These results indicated that TYLCV is not endemic to the Arava region, but rather wasa being introduced every year by an influx of whiteflies from the western parts of Israel. Unfortunately, there is no direct evidence for this hypothesis. However, whiteflies have been trapped in mid-August in the northern, desert part of the Arava at a distance of approximately 20 km from the nearest cultivated fields, which may indicate that the whiteflies are dispersed over great distances.

During June and July, local vector populations were found to be relatively low and the natural sources of TYLCV were scarce. Cultivated fields were found to be the major source of whiteflies in this region. Therefore, in order to reduce whitefly-transmitted viral epidemics (such as TYLCV), a vegetable crop-free period for those months was suggested. Indeed, following the implementation of a 2-month crop-free period in 1986, 20 years ago, there has been no TYLCV or any other vegetable virus epidemic in the Arava region (Ucko et al., 1998).

5. BREEDING FOR TYLCV RESISTANCE

Genetic resistance in the host plant is an ideal defense against whitefly-transmitted (as well as other) viruses, since it requires no chemical input and/or plant seclusion and can potentially be stable and long-lasting. Thus, the best way to reduce TYLCV spread is by breeding tomatoes that are resistant or tolerant to the virus. Since all cultivars of tomato (*Solanum lycopersicum*) are extremely susceptible to TYLCV, wild tomato species have been screened for their response to the virus (Lapidot & Friedmann, 2002). The first attempts at breeding for TYLCV-resistant tomato plants were made in the early 1970s using *S. pimpinellifolium* accession LA 121 as the resistant source (Pilowsky & Cohen, 1974). After a few years of repeated tries to introgress the resistance into the domesticated tomato (*S. lycopersicum*), the resistance level of LA 121 was found to be insufficient and efforts were shifted to accessions of *S. peruvianum*, which was found to express a higher level of TYLCV resistance. Indeed, in 1986, the first commercial TYLCV-resistant tomato hybrid TY20 was released (Pilowsky & Cohen, 1990; Pilowsky et al., 1989). The breeding efforts continued, and led to the development of highly TYLCV-resistant lines which do not exhibit symptoms following inoculation with TYLCV (Friedmann et al., 1998; Lapidot et al., 1997). Moreover, it was demonstrated that tomato lines expressing a high level of TYLCV resistance serve as a poor inoculum source for the virus

(Lapidot et al., 2001). Today, due to the continuous breeding efforts of a number of research groups, including the Volcani group, elite commercial TYLCV-resistant tomato hybrids are available (Lapidot & Friedmann, 2002).

6. CONCLUDING REMARKS

TYLCV spread very rapidly from its origin in the Jordan Valley to other parts of Israel and neighboring countries in the eastern Mediterranean, such as Cyprus, Egypt, Jordan, Lebanon, Syria, and Turkey. However, over the last decade, the geographic range of TYLCV has greatly expanded to include the western Mediterranean, Japan, the Caribbean, and the southeastern United States (Polston and Anderson, 1997; Polston et al., 1999; Moriones & Navas-Castillo, 2000). Today, TYLCV is a limiting factor in tomato cultivation worldwide. The reasons for its vast spread and its establishment as a worldwide menace are discussed later in this book.

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