INSECT VECTORS OF TRISTEZA VIRUS[1]

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HISTORY

The tristeza virus must have been in eastern and southeastern Asia for a long time. We cannot know surely, but it is reasonably probable that it originated in the same area as the cultivated species of citrus. It is also probable that the tropical citrus aphid, *Toxoptera citricidus* (Kirk.), originated in this area. This aphid has been known as the oriental citrus aphid, black citrus aphid, brown citrus aphid, pulgão preto, and pulgon negro, and has gone under the scientific names *Aphis citricidus* (Kirk.), *Aphis tavaresi* Del Guercio, and *Aphis citricola* van der Goot. The coffee aphid, *Toxoptera aurantii* (B. de Fonsc.), also seems to have originated in this area. It too has been called black citrus aphid, brown citrus aphid, and pulgon negro. The melon or cotton aphid, *Aphis (Doralina) gossypii* Glover, is world-wide in distribution, so probably it, also, has been in eastern Asia for a long time. These must have lived together and achieved such balance or tolerance that none were exterminated.

Early movement of citrus out from this center was by seed. The tristeza virus must therefore have been left behind. But since most citrus species only rarely produce a good variety by seed, growers learned to bud or graft citrus trees, and budwood and budded trees were carried around the world.

It is most probable that before 1890 the tristeza virus had been introduced into the United States (California and Florida), South Africa, Australia, and the Mediterranean Basin.

By this time the tropical citrus aphid had found its way into the islands of the East Indies and into the Hawaiian Islands, Australia, and South Africa. This aphid did not get to Florida or California and there is doubt as to when this aphid species arrived in South America east of the Andes Mountains. It was collected in Chile in 1911, but was not included in lists of citrus aphids in Argentina or Brazil until much later. There is no doubt that tristeza was widespread in South Africa by 1899, since trees of sweet orange on sour orange root planted that year by Davis (*7*) were quickly killed, as were many orchards of that combination planted about the same time. A similar condition seems to have existed in Australia. There is no evidence of spread of tristeza by insects in North or South America or in the Mediterranean Basin at that time.

In 1928 an effort was made to use sweet-on-sour orange trees in Java (*22*) with results similar to those observed earlier in South Africa. Both the tristeza virus and the black citrus aphid must have been well established in Java before that date.

By about 1930, tristeza was causing trouble in Argentina (*4*). The tropical citrus aphid also was present there and within a few years the disease had caused serious damage to Argentine citrus. Tristeza was first observed in Brazil in 1937 (*3*). In 1939 tristeza (quick decline) was first observed in California, and here for the first time the disease was found doing damage outside the range of the tropical citrus aphid. This

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was certainly at least 40 years after the introduction of the virus into this State, for it is now known that it was present in some of the early citrus importations brought in through the U. S. Department of Agriculture, Office of Foreign Plant Introductions.

Fawcett and Wallace (*11*) first demonstrated the virus nature of tristeza (quick decline) by reproducing the disease by means of tissue-graft transmission of the causal factor. The first experimental insect transmission of the tristeza virus was reported in 1946 by Meneghini (*18*), who showed that the tropical citrus aphid was a vector. This was confirmed by Bennett and Costa (*1*) in 1947. Hughes and Lister (*13*), in 1949, reported that the tropical citrus aphid transmitted the lime dieback disease in West Africa, while McClean (*16*), in 1950, reported that this same aphid transmitted the stem-pitting disease of grapefruit in South Africa. In 1949, McAlpin (*15*) reported transmission of bud-union decline by the black citrus aphid. In 1952, Fraser (*12*) reported the transmission of the seedling-yellows form of tristeza by this same *Toxoptera citricidus.*

Meanwhile, in 1951, Dickson, Flock, and Johnson (*9*) had reported that in California tristeza was transmitted by the melon (or cotton) aphid, *Aphis* (*Doralina*) *gossypii.* In 1954, Norman and Grant (*20*), working in Florida, confirmed the melon aphid as a vector and added the green citrus aphid, *Aphis* (*Doralina*) *spiraecola* Patch, to the list of tristeza vectors. In 1957 these same workers (*21*) reported that the coffee aphid, *Toxoptera aurantii*, also is capable of transmitting tristeza in Florida.

TYPE OF TRANSMISSION

Aphid vectors become infective during a short feeding period and lose their ability to transmit this virus rather rapidly when feeding on healthy citrus plants. Dickson *et al.* (*10*) reported that melon aphids could become infective during a feeding period of only 5 minutes on diseased orange leaves. They also reported that melon aphids lost their infectivity during a feeding period of not more than 2 hours on healthy orange leaves.

Costa and Grant (*6*), using tropical citrus aphids, got infections after acquisition feedings of 1 hour and inoculation feedings of 30 minutes. They also reported that infective tropical citrus aphids lost their infectivity in less than 24 hours when feeding on healthy citrus. Meneghini (*19*) reported that this aphid retains its infectivity for more than 24 hours but less than 48 hours when starved.

Tristeza virus seems to be transmitted from and to all its hosts by aphid vectors. All strains of tristeza are transmitted. Norman and Grant (*21*) reported getting a mild strain of tristeza from Meyer lemon in Florida. In California we have transmitted a severe strain of tristeza from Meyer lemon to lime by melon aphids. According to Wallace, this strain seems to be identical with the seedling-yellows tristeza known in Australia and recently discussed by him (*23*).

VECTOR EFFICIENCY

The tropical citrus aphid, *Toxoptera citricidus*, has been reported to be a rather efficient vector of the tristeza virus. Bennett and Costa (*2*) got 76.3 per cent infection by transferring colonies of 100 to 300 tropical citrus aphids. They also infected 2 out of 30 test plants (6.7 per cent) by transferring single aphids to them. Costa and Grant (*6*) obtained 16 per cent and 17 per cent infection with single aphids and got 88 per cent infection by colonies of more than 100 aphids. The rapidity of the natural spread of tristeza across South America (*5*) and the general infection in South Africa (*17*) added further evidence of the efficiency of this vector.

On the other hand, the melon aphid appears to range from a non-vector to a fairly efficient vector at various times and places. In Texas, Dean and Olson (*8*) reported that natural spread does not seem to be taking place and that an extensive series of tests with the melon aphid and the green citrus aphid resulted in no infections. A similar condition appears to exist now in the San Joaquin Valley in California and in the Mediterranean Basin. Although no experimental evidence can ever be presented, it would appear that the melon aphid was not a vector in southern California or Florida for a considerable period after the introduction of the tristeza virus into these states. This must also have been true in Florida for the green citrus aphid and the coffee aphid, and seems to be still true for these two species in California. Dickson *et al.* (*10*) reported rather low rates of transmission of tristeza virus by the melon aphid, obtaining only 6.3 per cent infection from colonies of 100 to 300 aphids, or about 70 per cent less than that reported by Bennett and Costa with colonies of the same size of the tropical citrus aphid. Even at the low rate of efficiency found in California, the population of melon aphids found there is high enough to account readily for the observed spread.

In Florida, Norman and Grant (*21*) have reported that the melon aphid, *Aphis gossypii*, and the green citrus aphid, *Aphis spiraecola*, are rather efficient vectors of the strains of tristeza virus present there.

The transmission of tristeza virus by membracids, reported by Dickson *et al.* (*9*), is in error. The symptoms observed were not caused by the tristeza virus. Reported transmission (*14*) of tristeza in Africa by the mealybug *Ferrisia virgata* (Ckll.) is based on a single experiment and needs confirmation by further work.

Differences in vector identity and efficiency in various areas are probably caused by differences in the virus strains present rather than in aphid strains. Natural selection will certainly favor a virus strain that is readily carried by the local aphids. Differences in transmissibility in various localities indicate that secondary introductions into a locality could be responsible for an outbreak or a new type of infection.

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