

Part III. The Bionomics of specific vectors of plant viruses.

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Introduction to: THE BIONOMICS OF SPECIFIC VECTORS OF PLANT VIRUSES

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This section is devoted to the vector relations of viruses and plants, and to the effects of processes of feeding sucking insects on plants. Such processes of feeding influence the transmission of viruses and may cause symptoms similar to virus symptoms.

Professor Vidano's lecture, which begins this section, enumerates cases of this type of damage which may be confused with virus diseases. There is similarity in leaf-symptoms between Pierce's disease of grapes and foliar burning of grapes caused by Empoasca species; Professor Vidano points out similarities and differences in symptoms. The vector of flavescence dorée, Scaphoideus littoralis, seems to have changed its feeding habits; in its native habitat in North America this leafhopper lives on weeds or perennials and is considered harmless, while in Europe it completes its life cycle on grapevines. The leafhopper is a harmless insect in the United States, but in its new home in Europe it transmits the flavescence dorée virus.

In his discourse on virus-vector-relationships, Professor Freitag describes progress in understanding the complicated connections between virus and the vector. For the epidemiology (epiphytology) of virus diseases, it is important to know the behavior of the virus in (or on) its vector from the first moment of uptake until the disappearance of the virus from the vector. We are at times inclined to make too many generalizations. Professor Freitag points out that there are more differences in the transmission of viruses by different groups of insects than generally is believed. The fatal effect of viruses on the vector, and the change of food qualities of plants for aphids and leafhoppers after virus infection, are examples of how this basic research may be of practical value.

In the third lecture of this section, Professor Frazier discusses factors of vector specificity of viruses transmitted by xylem feeders. As with aphid vectors, the cicads seem also to separate into groups that feed in, and transmit viruses to, specific tissues. It is astonishing, though, that so few viruses have properties like the viruses of Pierce's disease and phony peach. In light of accumulating knowledge, the supposed relationship between the two viruses seems doubtful.

D. Schvester mainly discusses ecological problems of vector and virus spread of *flavescence dorée* in southern France. It is astonishing that there are such differences in distribution of the virus disease and the vector. It may be that strains of *Scaphoideus littoralis* exist with different vector qualifications, or that an unknown vector is a transmitter in vineyards where this leafhopper is missing. The life history of this leafhopper on grape offers good possibilities for control measures, in spite of the long retention period for the virus within the vector. In respect to feeding habits, *S. littoralis* is put into a new group: "mixed feeders"; this species is not a strict phloem and not a strict xylem feeder--its stylets sometimes reach the phloem and sometimes reach the xylem.

Since discovering the ability of nematodes to serve as vectors of plant viruses, much progress has been made in our knowledge of the behavior of the viruses within the vector and modes of transmission. The discourse of Raski gives a good idea of the many facts on transmission of soil-borne viruses that have been determined in a short time. With insect-borne viruses, it took several years to reach this point in knowledge. It was not expected, with the first publication on nematodes as vectors of grape viruses by Hewitt, Raski, and Goheen in 1958 that 15 nematode species would be recorded as vectors by this time. Many questions are unanswered as to the nematode vector of plant viruses--the speakers who follow state some of the problems which urgently need further investigations.

RESPONSES OF *VITIS* TO INSECT VECTOR FEEDING*

Carlo Vidano

Various species of insects have been suspected or accused of being vectors of grapevine viruses. However, most efficient transmissions by insects from vine to vine were obtained by Auchenorrhynchous Homoptera. The grapevine viruses which are known to have insects as vectors are Pierce's disease and *flavescence dorée*.

Pierce's disease, up to now present only in North America, is spread naturally or experimentally transmitted by more than two dozen species of *Cicadellidae* or *Jassidae* (Hewitt *et al.*, 1942; Frazier, 1944; Frazier and Freitag, 1946; Freitag *et al.*, 1952; Stoner, 1953; Crall and Stover, 1957; Kaloostian *et al.*, 1962). Experimentally, this virus disease has also been transmitted by four species of *Cercopidae* or spittle bugs (Severin, 1947, 1950). The *flavescence dorée* up to now present only in Europe, and particularly in France, was transmitted during experimental trials by the leafhopper *Scaphoideus littoralis* Ball (Schvester *et al.*, 1961, 1963).

The *Cicadelloidea* of the Nearctic Region act as insect vectors of both Pierce's disease and *flavescence dorée*. In fact, even *S. littoralis* which has also been found in Italy (Vidano, 1964), is a native of North America. Here, this leafhopper has not yet been implicated as a grapevine species, while in Europe it breeds only on *Vitis*.

Among the Homoptera in general and the Auchenorrhyncha in particular, several species which are either habitual or occasional vine-inhabiters have not yet been investigated. A better knowledge of these grapevine-feeding

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insects is necessary to determine their specific responsibility for grape diseases and disorders. Such insects, besides being responsible as virus vectors, may be autonomous pathogenetic agents. They can cause remarkable disorders to the plants because of their particular piercing-sucking mouth structure. With their feeding punctures, the mechanical action of the stylets and toxicogenic action of the saliva occur (Carter, 1962), and plasmatic material is taken out of the pierced tissues.

The responses of the grapevine to the feeding of such insect-suckers are often noticeable. Sometimes they present pathological pictures which are striking but not always easy to diagnose. Worthy of mention are certain strange symptomatological coincidences between changes caused by leafhoppers and alterations due to other agents (Vidano, 1963 a).

Most of the species here considered are not accused of transmitting grapevine viruses. However, they are interesting because of various aspects, especially for the foliar and caulinar changes and disorders related to their feeding.

Froghoppers

The principal froghoppers or spittle bugs (*Cercopidae*) known in the virological field are *Aphrophora angulata* Ball, *A. permutata* Uhler, *Clastoptera brunnea* Ball, *Philaenus spumarius* L. (= *leucophthalmus* L.). These four species have been proved vectors of Pierce's disease virus (Severin, l.c.). Among them the most important is *P. spumarius*, or meadow froghopper, which lives commonly on the vines, although its life-cycle usually occurs on herbaceous plants. It is Holarctic in distribution, having been brought to the Nearctic Region from the Palaearctic one. Among the insects capable of transmitting Pierce's disease, the meadow froghopper is particularly interesting as it is the only one represented in both North America and Europe. In entomological literature it is indicated as a sucking insect occasionally injurious to grapevines. However, not much information exists about the responses of the vines to the feeding of this insect. Some results have been obtained with reference to adult attacks on vines grown from seeds (Vidano, unpublished data).

A simultaneous attack by three or four adults on the stem of a young grapevine seedling with 10 or 12 leaves may cause a quick scalding and drying of the apical leaves and the stem. This phenomenon usually occurs when the feeding punctures are made on a small part of the stem where the insects are confined in a small cage. The same pathogenetic effect also occurs when the experiment is made using the Cercopid *Lepyronia coleoptrata* L. Even a single specimen of *P. spumarius* can cause some disorder when it feeds on the part of the stem closed in a container. In this way the stem inside the container swells according to the number of feeding punctures. Often the leaves growing above the swollen area show marginal drying and sometimes downward rolling. But both these foliar disorders are never extensive.

P. spumarius is a typical xylem feeder. The apex of its mouth stylet usually reaches the xylem parenchyma and often enters into the lumina of the vessels. A large quantity of xylem sap is sucked, since a single adult may excrete 1.5-2 cubic centimeters of liquid in a 24-hour period. When the punctures are many in a limited area, all the pierced tissues (cortical and ray parenchyma, phloem, cambium, etc.) become severely injured. Then a remarkable hyperplastic phenomenon and a defective functioning of the phloem occur. Obviously the above quick foliar scalding and drying are caused by a lack of compensation in the water supply, while the eventual downward rolling occurs

because of the interference in the phloem tissue.

Treehoppers

Only a few species of treehoppers (*Membracidae*) are suspected or proven to transmit plant viruses (Heinze, 1959). One of them is *Microtalis* sp., which is a vector of pseudo-curly top virus in Florida (Simons and Coe, 1958; Maramorosch, 1963). No treehopper species has been proved to be a vector of grapevine viruses. Worthy of mention are certain strange pathological manifestations caused on the *Vitis* by *Ceresa bubalus* F., or buffalo treehopper, the ampelophily of which has recently been noted in Italy (Vidano, 1963 c). This Membracid, Nearctic in origin but now widely distributed in Europe, is well-known for the injury caused to fruit trees by its egg-laying slits. On the vines, it causes surprising caulinar and foliar changes, which are related to its particular kind of feeding (Vidano, 1963 b).

The pathogenetic process occurs when a large number of well-defined feeding punctures encircles shoots, lateral shoots, and canes. In the tissues pierced by the buffalo treehopper there remain evident traces-- yellowish-brown feeding tracks or sheaths which clearly indicate the route taken by the stylets bundle. The insect is, above all, a phloem-sucker (or at least a phloem-destroyer) although it also damages other tissues. The tip of its stylets can reach the xylem parenchyma, the vessels and the pith, but only in the thin shoots. However, the buffalo treehopper does not appear to be a skillful xylem-sucker when it feeds on vine shoots that stand in a diluted solution of safranin (1 o/oo).

Irregular punctures do not normally result in a marked reaction; on the contrary, the pathological phenomenon takes place where many feeding tracks are aligned in one or more rings or spirals. At the level of these sheaths, which radially penetrate the tissues of the affected shoots, there begins a degenerative process followed by necrosis in the phloem and the cambium. In the herbaceous growths, or shoots, the epidermis and the cortical parenchyma are also subjected to necrosis, resulting in a considerable brownish annular strangling which appears externally. In the woody growths, or canes, the ring alteration remains hidden (at least initially) under the dead outer layers of bark already formed at the time of attack. At the trauma level, scarring processes, sometimes very marked, take place and eventually expose the annular alterations even in mature canes when the bark splits longitudinally.

The radially pierced shoots and canes undergo a remarkable traumatism in the conducting elements of the phloem (the xylem remains undamaged). Then, the excessive accumulation of metabolized material, consisting mainly of carbohydrates, causes remarkable changes of the various organs situated above the point of the trauma. The most involved organs are the leaves, which undergo downward rolling, thickening, brightening and yellowing or reddening.

Many woody plants are pierced by the buffalo treehopper, but none of them responds in such a way. Reactions like that of the grapevines occur instead on herbaceous plants, and particularly on *Medicago sativa*.

It is interesting to note that foliar changes similar to those caused by *C. bubalus* occur on the vines pierced by the scale insect *Icerya purchasi* Mask. In this case the pathogenetic process also begins at the level of the punctures made on the shoots (frequently, leaf stalks are also involved), and damages the phloem tissue annularly (Vidano, unpublished data).

Sharpshooters and Leafhoppers

The main sharpshooters and leafhoppers involved in the field of grapevine virus diseases and disorders belong to the families *Cicadellidae*, *Deltocephalidae* and *Typhlocybididae*. More than two dozen sharpshooter and leafhopper species have been recognized as vectors of Pierce's disease virus. Some of them are grapevine-inhabiting, at least as adults, and are more responsible for spreading the disease. With the exception of *Oncometopia undata* F., which causes damage by its egg-laying slits (Müller, 1956), these cicadellids are not known to injure the grapevine as primary pathogenetic agents. They are xylem-sucking insects and excrete a large quantity of liquid when feeding on succulent shoots. In reference to the *Draeculacephala minerva* Ball, which lives on *Vitis* as an adult only, it was recorded that "the excrement from a single individual female amounted to as much as 2.5 cubic centimeters in a 24-hour period". (Houston, Esau and Hewitt, 1947). Regarding *Horcna circellata* Baker, which is grapevine-inhabiting both as adults and as nymphs, it has been said that "large populations of the blue-green sharpshooter can occur on grapes and more than 1000 nymphs have been counted on a single vine" (Freitag and Frazier, 1954); and that "when *H. circellata* was abundant on shrubs and trees in a Berkeley garden, the feces dropping from nymphs and adults resembled a fog" (Severin, 1949). In spite of this, neither *D. minerva* nor *H. circellata* appear to be listed among insects which cause damage to grape by feeding only.

No Nearctic cicadellid species involved in Pierce's disease transmission were found in Europe. A species taxonomically near these species is *Cicadella viridis* L., or green leafhopper, which breeds on various herbaceous plants. In its natural environment the adults feed commonly on vines but they do not cause evident disorders. In experiments, vines subjected to intense attacks by this leafhopper have never given clear symptoms (Vidano, unpublished data).

A grape-inhabiting leafhopper worthy of particular mention is *Scaphoideus littoralis* Ball. This species has been introduced into Europe from North America (very probably in the egg stage) by vine canes. It is interesting to note that in Europe, *S. littoralis* transmits a grapevine virus (Schvester *et al.*, 1961 and 1964), flavescence dorée virus (Caudwell, 1957 and 1964), while in North America it is not even known as a grape-inhabiting species (DeLong, 1948; Beirne, 1956).

S. littoralis breeds once a year and overwintering occurs in the egg stage, usually in the bark of 2-year-old canes. Both nymphs and adults live mainly on the lower surface of the leaves. They feed almost continuously, inserting their stylets into the leaf ribs. Leaf stalks and herbaceous shoots are also involved. At the points of puncture, brownish patches appear in the ribs, and some hyperplastic and hypertrophic reaction occurs in the herbaceous shoots. The apex of the stylets always reach the conducting tissues. Some immediate effects of the feeding punctures have been investigated by using diluted colored solutions (eosin, safranin and green iodine at 1 o/oo). The act of sucking usually involves the mechanism of the xylem-sap movement, even when the woody vessels are not directly affected. Microscopic examination of the pierced organs shows that *S. littoralis* is usually phloem-damaging rather than xylem-damaging (Vidano, 1964).

In the field it is not easy to ascertain symptoms due to *S. littoralis* attacks. Vine alterations caused by this leafhopper as an autonomous pathogenetic agent were obtained in laboratory tests by using "non-viruliferous" specimens raised from eggs and "healthy" plants suitably isolated from the outside environment. In this way, vines heavily infested had their growth severely

restricted. The foliar symptoms were thickening of the blade, downward rolling of the edges and precocious yellowing. In addition, traces of marginal burning appeared on the more infested leaves. However, such foliar symptoms were inadequate in comparison to the intensity of the attacks. Equally intensive attacks by *Empoasca* (*E. flavescens* and *E. libyca*) cause more serious disorders.

Many phytopathologically important species of grapevine-inhabiting leafhoppers belong to the genera *Erythroneura*, *Zygina*, *Arboridia* and *Empoasca* (*Typhlocybidae*). Their geographical distribution is very interesting. The numerous species of grapevine-inhabiting *Erythroneura* (*E. comes* Say, *E. tricineta* Fitch, *E. ziczac* Walsh., etc.) are Nearctic in distribution. The only species of *Zygina* (*Z. rhamni* Ferr.) so far known living normally on grapes is distributed in the Mediterranean countries. The grapevine-inhabiting *Arboridia* (*A. adanae* Dlabola, *A. dalmatina* Novak Wagner, *A. kermanashah* Dlabola, etc.), all of them found recently, live in the Balkan Peninsula and southwestern Asia. Finally, the grapevine-inhabiting species of *Empoasca* are *E. flavescens* Fabr. and *E. libyca* Bergevin. The first is widely distributed in Europe, while the second is found mainly in North Africa.

The above-mentioned species have not been implicated in the transmission of grapevine viruses. Nymphs and adults of *Erythroneura*, *Zygina* and *Arboridia* species inhabit the lower surface of the leaves. They pierce the mesophyll tissue and empty groups of palisade cells, and characteristic white spottings appear on the upper leaf surface. Very different (and generally more pronounced) are changes caused by the two species of *Empoasca*, although their feeding apparently resembles that of the other Typhlocybrids living on vines.

Empoasca flavescens and *E. libyca* are small green leafhoppers which generally inhabit (both as adults and nymphs) the lower surfaces of leaves, and which feed by piercing the ribs. Sometimes leaf-stalks and tender shoots are also pierced, mainly by adults. The alterations, chiefly the foliar alterations, caused by the two species of *Empoasca* are surprisingly manifest and heterogeneous. The most important symptoms are scalding, burning, downward rolling, thickening, brightness and yellowing or reddening. Generally these foliar changes start from the edges and progress toward the petiolar sinus. In any case, the changes are always associated with a symptomatic vein browning which appears only when the leaves are examined against the light either in those showing marginal burning or downward rolling.

Vein browning is the first symptom of the *Empoasca* attacks. It is caused by the pathogenetic effect of a number of feeding punctures. Longitudinal sections and cross sections of darkened veins show striking strips and patches of an abnormal material (yellowish or brownish-yellow in color when fresh and similar to gum, surrounding the apex of the leafhopper sheaths. The phloem is always injured. The cortical parenchyma and the xylem parenchyma are often involved. The vessels remain undamaged, although the insect is able to suck their sap (Vidano, 1963 a).

Vein browning is not a systemic change, though it usually progresses from the leaf edge to the petiolar sinus in all the leaves of an infested vine. By compelling the *Empoasca* to feed on pre-established foliar areas in cages and containers, vein browning occurs only in the ribs that may be reached by the stylets of the insect. The intensity of the vein browning and of the successive leaf change is directly proportional to the number of the feeding punctures. Weak and slow infestations mainly cause a progressive obstruction in the phloem-conducting tissue. Then the reaction of the affected leaves is subsequently down rolling of the edges, thickening of the blade, brightness of the upper surface, and reddening or yellowing. All these mentioned symptoms are clearly

related to the arrest of the downward movement of the phloem saps, or to the excessive accumulation of elaborated organic material. On the other hand, strong and sudden attacks (particularly during the hot and dry season) cause alterations related to the interference in the ascent of the xylem sap. In the affected leaves, scalding and burning starting from the edges occur then.

Vines severely infested by *Empoasca* can show a remarkable slowing of growth, but usually they become vigorous again if the infestation does not re-occur in successive years.

Discussion and Conclusions

As far as is presently known, the responses of *Vitis* to the feeding insect vectors of grapevine virus are somewhat limited. In regard to the principal vectors of Pierce's disease, there was no indication of vine damage induced directly by these species. Some foliar and stem disorders were, however, noted on vine seedlings infested by *Philaenus spumarius*. The only known vector of flavescence dorée, *Scaphoideus littoralis*, causes alterations in grapevines, but not so intensive as one would expect. On the contrary, remarkable responses of *Vitis* occur when the attacks are due to certain piercing-sucking insects not proved to be grapevine virus vectors. Such insects have been implicated as being primarily pathogenetic or autonomous agents. Often they induce the appearance of external symptoms similar to those due to other pathogenetic agents, viruses included.

Of much significance is the similarity between the foliar burning of vines infested by *Empoasca* and that of vines affected by Pierce's disease. In both cases the xylem-conducting tissue is involved, but in two different ways. In the vines affected by Pierce's disease, the vessels become plugged by gum and tyloses, both in the herbaceous and woody organs. The diseased vines die 2-4 years after having shown the first symptoms. In the vines infested by *Empoasca* the vessels remain undamaged and the lack of compensation in the water supply occurs only at the level of the pierced herbaceous organs. The severely hit vines show a remarkable dwarfing, but they can become vigorous again the next year if other *Empoasca* attacks do not occur.

Also significant is the similarity between the downward leaf rolling due to insect feeding punctures, and that induced by other causes--including virus diseases such as leaf roll and flavescence dorée. Such foliar malformation is notoriously induced by disturbances of the phloem-conducting tissue. In the vines affected by virus diseases, the non-functioning of the phloem may be either systemic as in leafroll or irregularly systemic as in flavescence dorée. In vines in which the downward leaf rolling is only caused by insect feeding, the disturbances of the phloem tissue clearly involve only certain parts of the infested plant. The best examples are the attack effects of *Ceresa bubalus*, *Empoasca* (*E. flavescens* and *E. libyca*).

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