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Studies on Virus Diseases of the Grapevine in California

by

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Introduction

Grapes are one of the most extensively planted and important fruits of the world. The generous exchange of varieties and rootstocks among countries has resulted in a similar but incognizable distribution of diseases of the grapevine. Many of the virus diseases of the grapevine thus have been taken to different countries. Those found in vineyards of California are similar to the virus diseases of cultivated grapevines in many of the other vineyards of the world.

Some of the viruses like those that cause Pierce's disease (Hewitt, 1953) and flavescence dorée (Caudwell, 1957 and Gärtel, 1959) kill many grapevines and are cause for much alarm and attention. Whereas most of the other viruses of grapevines cause diseases that are more insidious, they are less dramatic; they affect the amount and quality of crop, bring about vine degeneration, and even may render the soil unfit for replanting to grapevines.

Identification, modes of spread, and control of virus diseases which attack the grapevine are problems common to all the countries of the world that produce grape.

This paper describes the virus diseases found in vineyards of California. Efforts are made to liken California-named virus diseases to similar diseases described in the literature, but no attempt is made to review all of the literature or to catalogue the different world-wide diseases of grapevines. It contains the first report of transmission of the corky bark disease and the initial description of an unidentified symptom called fleck. It also includes the first report of nematode transmission of the grape yellow mosaic virus, a discussion of probable strain relationships in the soil-borne viruses, and a report on chemical soil treatment tests in California.

Virus Diseases of the Grapevine in California

The virus diseases may be arranged in many different ways. In this discussion they are grouped by modes of spread. Virus diseases that spread naturally in vineyards of California are Pierce's disease, fanleaf, yellow mosaic, and vein banding. Though on occasions there has been indication of spread of leafroll in parts of California, precise evidence of spread is lacking. There is no evidence or indication of natural spread of asteroid mosaic, corky bark, yellow vein, or enation.

Spread through Air

Pierce's d i s e a s e. This disease kills most varieties of grape *Vitis vinifera* and *V. labrusca* (Hewitt, 1953). The disease has been found in gulf coast states and California and has been reported in Mexico and Argentina (Hewitt, 1958). It is the only virus disease affecting grapevines in California that is known to be spread by air-borne vectors.

Scalding and burning of the leavers are the first symptoms of the disease to show after inoculating a grapevine either by vectors or by grafting. Portions of the margins of the leaf, most often near a large vein. dry while green and later turn brown. Borders of the affected tissue turn yellow or red. The burning progresses, often in concentric zones, from the margins toward the petiole. Fruits which develop on canes that show leaf symptoms may or may not size fully before withering and drying up. Fruits often color prematurely before withering. Canes mature irregularly in brown and green patches, and the leaves drop, leaving petioles attached to the canes. The second and later seasons of disease are characterized by delayed growth and interveinal chlorosis of the basal four to eight leaves, followed in midsummer by leaf burn and other symptoms just described. Death of roots usually follows closely the decline of the top (Hewitt, 1953).

Spread through Soil

There are three known soil-borne virus diseases of grapevines in California. These are fanleaf (Hewitt, 1950), yellow mosaic (Hewitt and Delp, 1953), and vein banding (Goheen and Hewitt, 1962). The diseases are often found as a complex, concentrated in defined areas of vineyards, and appear to spread slowly from the margins of the area. An example is discussed later under yellow mosaic.

F a n l e a f. This disease is apparently the same as 'arricciamento (Petri, 1929; Baldacci et al. 1961), urticado (Dias, 1950a, c), court noué (Vuittenez, 1956), and Reisigkrankheit (Brückbauer, 1957; Wilhelm, 1955). It is apparently a component of degénérescence infectieuse (Bovey, 1958). Leaves are deformed, and the margins toothed as are leaves of *Urtica,* suggesting the name "urticado" (Dias, 1950a). The sinuses are deeply cut or lobed, and the leaf blade is asymmetric. The petiole sinus is open wider than is normal; in some leaves it may open to as much as 200 degrees (Fig. 1, C). It is this symptom, with the primary veins growing closely together and resembling the ribs of a partially closed fan, that suggests the name fanleaf (Hewitt, 1950, 1954). Leaves are often mottled to different degrees in varying patterns and shades of green. They may show line patterns and feather veins (Fig. 2) which are primary symptoms of the disease, those which show first in test plants after inoculation either by grafting or by nematode vector.

Canes of grapevines may display different degrees of malformation — short internodes, double nodes, fasciation, zig-zag growth between nodes, and flat canes (Hewitt and Gifford, 1956). Trabeculae are found in the phloem and xylem cells of canes of diseased vines (Gifford et al. 1956).

Fruit set is often poor, resulting in straggly clusters with large seeded berries and small seedless berries.

Y e l l o w   m o s a i c. The diseases panachure (VUITTENEZ, 1952; GÄRTEL, 1954) and clorose infecciosa (DIAS, 1950b, 1955) are similar to yellow mosaic found in California. Yellow mosaic is characterized by chrome-yellow leaves and shoots in the spring. Later in the season it is also characteristic for the chrome-yellow mottle to vary in degree and pattern (Fig. 3, A, B); leaves may be completely yellow, have many yellow blotches, or only a few small, irregular yellow spots (HEWITT, 1945). Feathering of veins, broad vein banding, and light yellow green mottling are not uncommon. In hot weather, yellow leaves fade to
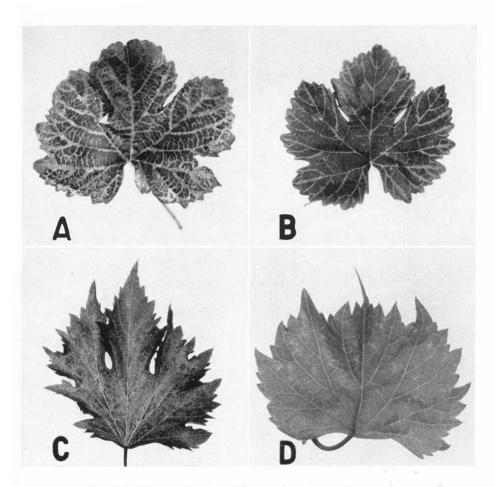

Fig. 1: Symptoms of virus diseases in leaves of grapevines

A, veinbanding; color, chrome-yellow; variety Grey Riesling; B, veinbanding; color, light green; variety Thompson Seedless; C, fanleaf; mottle light green prominent teeth, open petiole sinus; variety Mission: D, fleck symptoms, third-order veins, variety St. George
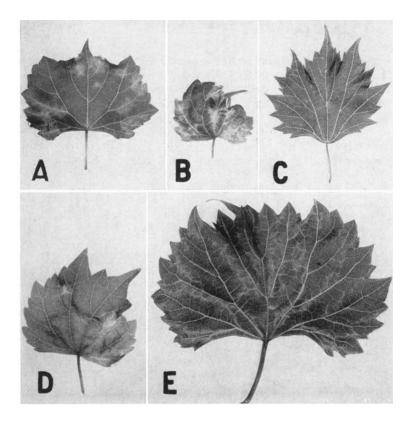
Fig. 2: Symptoms of fanleaf disease in leaves of *Vitis rupestries* var.
St. George

A, B, D and E. primary symptoms that show first after inoculation:
A, B and D variations in feather vein; E. line pattern; C, secondary
symptom, leaf deformity and deep marginal sinuses and prominent teeth

cream color and often burn or turn brown and may drop. As the weather warms
new growth develops with more nearly normal green leaves that may or may
not be variegated with yellow. Vines of some varieties with yellow mosaic may
also have deformed leaves, and canes with double and short internodes. In
addition to showing symptoms common to yellow mosaic expressed in many
varieties of *V. vinifera*, leaves of vines of *V. rupestris* var. St. George that have
been chip-bud-graft-inoculated with yellow mosaic commonly show line
pattern, and later nettle leaf symptoms associated with the fanleaf disease in
this variety. The clusters on vines with yellow mosaic are smaller than those
on normal vines and often straggly with many small seedless berries. Vines
with yellow mosaic gradually degenerate as do vines having fanleaf.

Spread of yellow mosaic occurs mostly at the margins of infested areas.
Figure 4 illustrates the spread of yellow mosaic in a nonirrigated vineyard in
Sonoma County, an area where it seldom rains much between May and

October. In this vineyard the rows and vines are eight ft apart. The figure shows the distribution of diseased vines in 1950 and 1959. Disease spread from the margins was about 32 ft during the 10-year period. During this time the disease also jumped eastward about 48 ft to a new spot and has subsequently spread in this area to other vines.

V e i n   b a n d i n g. Chlorotic bands along the veins, either light green (Fig. 1, B) or chrome-yellow (Fig. 1, A), are the primary characteristic of this disease. It may develop in early season, but more likely it becomes prominent after midseason or near fruit harvest (GOHEEN and HEWITT, 1962). Vines affected with vein banding produce less fruit than do normal vines. The clusters are straggly, with small seedless berries and a few large seeded berries.
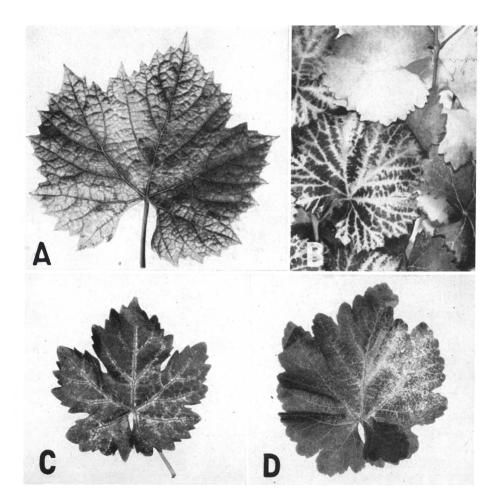

Fig. 3: Symptoms of virus diseases in leaves of grapevines, color chrome-yellow

A, B, yellow mosaic in varieties Pinot blanc and Grand noir; C, D, yellow vein in varieties Carignane and Emperor
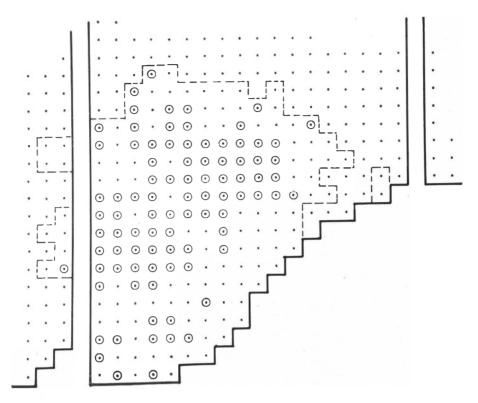
Fig. 4: An illustration of the distribution and spread of yellow mosaic in a vineyard in Sonoma County, California

Solid line is the margin of vineyard, circles indicate diseased vines in 1950, short dashes indicate outer limit of spread of yellow mosaic in 1959

Mode of Spread Undetermined

L e a f r o l l. Rollkrankheit (SCHEU, 1936) and white Emperor (HARMON and SNYDER, 1946; GOHEEN, HARMON, WEINBERGER, 1958) are the same as leafroll. A downward roll of the leaf margins is the principal symptom of the disease (Fig. 5). The degree of roll varies with the variety and shows first about mid-season in the older leaves at the base of the canes (GOHEEN, HEWITT, and ALLEY, 1959). As the season advances, roll develops in other leaves progressively toward the tip of the cane. Rolled leaves are often crisp, and crack when crumpled in the hand. Also, rolled leaves of red and black grape varieties develop premature fall red color, while leaves of white or green varieties are light green. Burning of the leaves is common on diseased vines in the hot interior valley climates of California (GOHEEN, HARMON and WEINBERGER, 1958). There does not appear to be any specific pattern to this leaf burn.

Most of the rootstock varieties, for example St. George, AXR, 99 R, 5 BB, 1613, 1202, and others, are symptomless carriers of the leafroll virus. The only

way to detect the presence of the leafroll virus in these plants is to index them on suitable indicator plants.

Leaves of *V. vinifera* varieties which are rolled are usually high in carbohydrates (GOHEEN and SCHNATHORST, 1961) and deficient in potassium, whereas the petioles are high in potassium (COOK and GOHEEN, 1961).

Fruit of diseased red varieties, and of some diseased black varieties, usually will not develop the full color of normal vines. The disease was formerly known as white Emperor, white Cardinal, or white Tokay because the fruits of diseased vines remained green or only developed a pink color (GOHEEN, HARMON and WEINBERGER, 1958). At harvest time, the fruit of diseased vines is often lower in sugar than the fruit of healthy vines. The difference may range from one to near four degrees Balling. Diseased vines also have less fruit than do healthy vines (GOHEEN and COOK, 1959).

Y e l l o w   v e i n. It is easy to confuse this disease with yellow forms of vein banding. Perhaps yellow vein is the same as some forms of coulure or colatura. Leaves on vines with the yellow vein disease may or may not show clear symptoms. Often, many leaves must be examined before one with
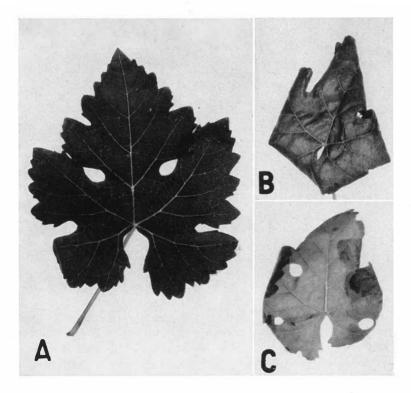

Fig. 5: Leaves of variety Burger

A, upper surface of normal leaf; symptoms of the virus disease, leafroll, B, upper, and C, lower surface

symptoms is found. Chrome-yellow veins were used by Hewitt (1956) to charac-
terize the disease (Fig. 3, C, D) though straggly clusters may have been equally
characteristic. Leaves may have different forms and degrees of yellowing. In
the variety Carignane, the yellow will often show as a mealy vein banding
(Fig. 3, C) or as yellow spots splattered loosely over the surface; in Emperor the
leaf veins become yellow (Fig. 3, D). The chrome-yellow color, however, has
been constantly associated with the disease.

On occasions, young leaves show a mild chlorotic mottle in an oak leaf line
pattern which fades as the leaves age. Straggly clusters with large, seeded
berries and small, seedless "shot berries" are common in diseased vines of
varieties Emperor, Carignane, Valdepenas, and Grenache. It is not uncommon
for clusters of the latter three varieties to dry up after bloom (Gooding, 1962).
Often vines with yellow vein will be larger than normal vines, and thus can
be distinguished at a distance from other vines in the vineyard.

A s t e r o i d   m o s a i c. Perhaps true mosaic (du Plessis, 1950) is similar
to this disease. Symptoms are distinctly different from those of the other known
virus diseases of grapevines in California. Leaf symptoms are characterized by
numerous small, lucid, third-order veins which often coalesce to centers form-
ing star-like spots (Hewitt and Goheen, 1959). When very numerous, these spots
fuse and tend to be more frequent between the primary and secondary veins
(Fig. 6, A). Leaves are often asymmetric, twisted, and puckered along the veins;
marginal sinuses are deeply cut, and blisters of normal green occur in leaves of
some varieties. During the summer at Davis, California, leaf symptoms become
less severe in most varieties tested. In leaves of St. George, the virus produces
yellowish, slightly enlarged primary veins (Fig. 6, B). Affected vines are often
stunted and produce little or no fruit.

C o r k y   b a r k. This is the first report of the virus nature of corky bark.
Corky bark was graft-transmitted to a seedling known at Davis as LN 33 from
Carignane, French Colombard, and Grenache vines that did not show symptoms.
In current season canes of LN 33 the bark is thick, spongy, and soft, and often
splits into longitudinal cracks that heal from the margins to form fissures as
the canes mature (Fig. 6, C, D). In older wood the bark becomes very rough.
Leaves on LN 33 vines with corky bark often become pinkish, they tend to
droop, and do not stand out normally from the cane. The canes on diseased vines
are greenish, poorly matured, and limber or rubbery.

A Virus-Like Disease

E n a t i o n. (To date this disease has not been experimentally transmitted
in California.) A similar disease occurs in southern Italy (Graniti, 1959; Cicca-
rone, 1961). Enation disease is characterized by the formation of leaf-blade-like
outgrowths on the lower surface of leaves (Fig. 6, E). Leaves with enations are
usually misshapen, dwarfed, and rough (Hewitt, 1954). The veins appear to be
larger than normal and are prominent on the lower surface. Enations have been
found most frequently on the first 8 to 10 leaves at the base of the canes. Other
leaves at the base of canes of diseased vines are nearly round, and have a
leathery texture. In the variety Tokay, the first 8 to 12 inches of shoots tend

to grow downward. The tips then turn up, and the canes appear to grow normally.

An Unidentified Symptom

F l e c k. Fleck is a symptom, graft-transmissible from certain grape plants to *V. rupestris* var. St. George. In the indexing of various selections of different varieties, it is not uncommon to transmit an apparent virus to St. George that produces a vein break in the third-order veins of the leaf (Fig. 1, D). The symptom has been called "fleck". It has been transmitted from *V. vinifera* vines without symptoms, and from vines with symptoms of vein banding and mild forms of fanleaf. The virus that produces the fleck symptom has not been identified nor has the symptom been correlated with a known disease.
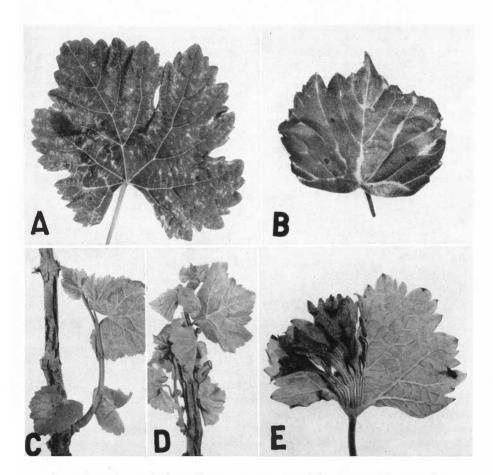

Fig. 6: Symptoms of virus diseases and a virus-like disease of grapevines

Asteroid mosaic in variety A, Merlot, and B, *V. rupestris,* var. St. George; C, D, corky bark; and E. enation, a virus-like disease

Methods of Transmission of Viruses Causing Diseases of Grape

A transmissible entity that can be moved from tissue of a diseased plant to a healthy plant and there increase and reproduce the disease, coupled with the failure to demonstrate the presence or the causal relationship of a microorganism to the disease, has been accepted as reasonable proof of a virus-caused disease.

Transmission by Grafting

Reports of transmission of the grape viruses by grafting from grapevine to grapevine are numerous. Cifferi, Corte and Scaramuzzi (1959) report transmission of infectious degeneration from grapevine by chip-budding to four species of woody plants, privit *Ligustrum lucidum,* buckthorn *Rhamnus purshiana*, mahaleb seedling *Prunus cerasifera* var. *divaricata* and mazzard F 12/1 cherry.

In California the following methods of graft transmission of grape viruses from diseased to healthy vines have been tested: 1) Approach grafting a cane from a diseased vine to a cane of a healthy vine; 2) top grafting a diseased scion onto a healthy base, either cutting or rooting; 3) top grafting a healthy scion bud onto a diseased base, either cane or rooting; 4) sandwich grafting a piece of diseased cane into a healthy cane or rooting; and 5) chip-bud grafting a bud and chip of diseased cane into a healthy cane or rooting. Transmission of several of the different grape viruses has been demonstrated by each of these techniques. However, chip-bud grafting has given more uniform, consistent and, in general, quicker results than have the other techniques. The method is reliable, simple, and excludes most criticism that may be applied to some of the techniques.

Transmission by Sap Inoculation

Cadman, Dias, and Harrison (1960) reported sap transmission of fanleaf and yellow mosaic viruses from leaves of grapevines to herbaceous plants, and graft transmission of the fanleaf virus from herbaceous plants back to grapevines. Viruses transmitted from leaves of yellow mosaic and fanleaf-diseased grapevines which they obtained from Portugal, France, Switzerland, and California all produced similar symptoms on the herbaceous plants.

Three papers from Milan, Italy, Amici, Baldacci, and Refatti, 1958; Baldacci et al. 1960; and Baldacci et al. 1961) report transmission of virus from grapevines to herbaceous plants. The last paper, in addition to presenting new research, summarizes the work carried out over the period 1958 to 1960. The authors report transmission, using various methods including sap inoculation, of fanleaf and yellow mosaic-like viruses from grapevines to several different species of herbaceous plants. By chip-bud grafting from some of the sap-inoculated herbaceous plants virus was moved back to grapevines and there reproduced the disease. Papers by Vuittenez (1960a) and Brückbauer and Rüdel (1961a, b, c) also report transmission by sap inoculation of virus from grapevines to herbaceous plants. ·

STRANÁK, BLATTNÝ, and KLEČKA (1931) and BLATTNÝ, STARÝ and NEDOMLEL (1956) report mechanical sap inoculation of the Melnik mosaic virus from grapevines to herbaceous plants.

OCHS, in a series of papers (1955, 1957, 1958a, c, 1959 and 1960 a), reported transmission of viruses from grapevines to herbaceous plants; however, the validity of her work has been questioned by NIEMEYER and BODE (1959), EHRENHARDT and BRÜCKBAUER (1959), and by HOPP (1959a, b, and 1961).

At Davis, California, we have transmitted viruses to herbaceous plants by mechanical sap inoculation from vines with fanleaf, yellow mosaic, vein banding, and yellow vein, but not from vines with other virus diseases.

Three ways of preparing sap from virus diseased grapevines for mechanical inoculation to herbaceous plants have been used and found to be equally suitable: 1) leaves were macerated in 2.5 per cent nicotine solution as in the method of CADMAN et al. (1960); 2) young leaves and shoot tips were macerated in 0.1 M K_2HPO_4 + KH_2PO_4 solution pH 7; and 3) root tips 1 cm long were macerated in buffer. The root tips from greenhouse plants, or forced cuttings, have in most cases been a good source of virus for mechanical inoculation. Leaves of herbaceous plants were dusted with corundum powder and rubbed with the sap in the usual way.
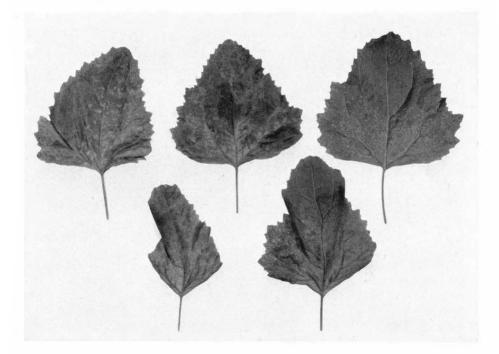

Fig. 7: Symptoms produced in leaves of *Chenopodium amaranticolor* by mechanical sap inoculation from leaves of grapevines with fanleaf. The inoculated leaves did not show symptoms
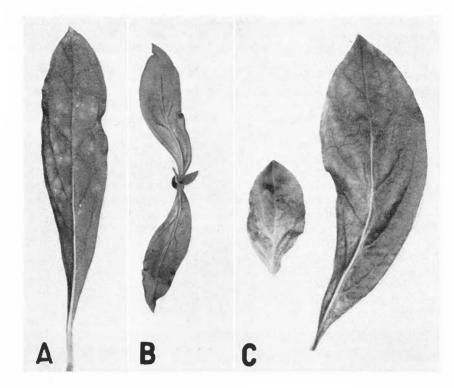
Fig. 8: Symptoms produced in leaves of *Gomphrena globosa* by mechanical sap inoculation from leaves of grapevines with fanleaf

A, inoculated leaf showing light chlorotic spots that often turn red with age; B, C, mottling and twisting on younger leaves

Grape fanleaf virus (GFV). Over the past two years, 1960 and 1961, the GFV has been transmitted by sap inoculation from vines to young seedling plants of the following: *Amaranthus retroflexus* L.; *A. tricolor* L. var. Molten fire; *Phaseolus vulgaris* L. var. Bountiful; *Cucumis sativus* L. several varieties; *Gomphrena globosa* L.; *Nicotiana clevelandii* Gray; *N. attenuata* Torr.; and *Erodium macrophyllum* Hook & Arn.

In *Chenopodium amaranticolor* Coste & Reyn. the GFV becomes mostly systemic and produces a mosaic mottle that shows first at the base of the second or third leaf from the apex (Fig. 7). In addition, sap inoculations from some grapevines produce rather severe symptoms of puckering and twisting of the terminal leaves (Fig. 7). We have observed in *C. amaranticolor* that symptoms may show any time from 7 to 30 days after inoculation, perhaps related to season, temperature, or other undetermined factors.

The GFV which is sap inoculated from vines to young plants of *G. globosa* becomes systemic and the symptom first observed is twisting of the two, small, opposite apical leaves of the shoot. As the leaves develop, they are usually mottled and remain twisted (Fig. 8). Sap inoculations from some grapevines

produce chlorotic local lesions in the rubbed-sap-inoculated leaves. As the leaves age, these areas turn red and then fade to red-purple. In *A. hybridus* L. and *A. tricolor* var. Molten fire, the GFV becomes systemic and produces a mild mottle that shows first in the base of the young leaf. The symptom moves from the base toward the tip. The virus also produces a mild mottle in *N. clevelandii* and *N. attenuata*. GFV sap inoculated onto cotyledon leaves of young seedlings of *C. sativus* produces small, light cream chlorotic spots that spread and become diffuse as the leaves age. The virus becomes irregularly systemic in the plant and produces a variety of symptoms, including chlorotic patches, feather vein, chlorotic oak leaf patterns, and a fleck in the leaves. Local lesions in sap-inoculated cotyledon leaves of *C. sativus* varieties Mincu and White Wonder are clear, distinct, small, light chlorotic spots that become necrotic. These plants produce local lesions with strains of the GFV and can apparently be used to indicate virus concentration.

Grape yellow mosaic virus (GYMV). Sap inoculations from leaves of eight different collections of grapevine with yellow mosaic have produced symptoms in *C. amaranticolor* and *G. globosa* that are similar to those produced by sap inoculations from vines with fanleaf disease; yet some
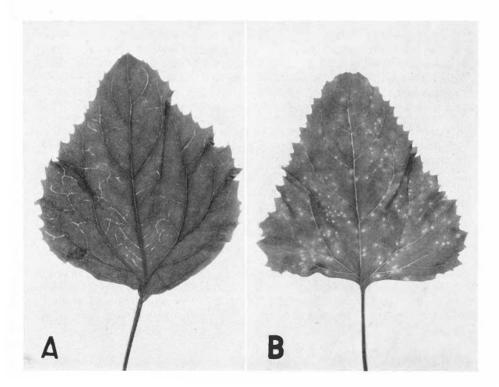

Fig. 9: Symptoms produced in leaves of *Chenopodium amaranticolor* by mechanical sap inoculation from leaves of grapevine with yellow vein

A, leaf from position on plant below inoculated leaf after about 20 days; B, inoculated leaf showing necrotic local lesions

collections produce faint yellowish veins in the upper leaves in *C. amaranti-color*.

Grape vein banding virus (GVBV). Similarly, sap inoculations from 12 different vines of nine different varieties with the vein banding disease have also produced symptoms in the above two species of herbs that are not different from those produced by the GFV.

Grape yellow vein virus (GYVV). Sap inoculations from leaves of vines with yellow vein to *C. amaranticolor* produce small, distinct, local lesions in 3 to 5 days in the sap-rubbed leaves (Fig. 9) (Gooding, 1962). The virus becomes systemic, producing severe twisting and distortion of the shoot apex and terminal leaves. The tip usually dies back 1 or 2 inches. Later side shoots develop with mottled and cupped leaves. The older leaves on the plant, if held for about 60 days, develop yellow veins (Fig. 9). The virus also sap-inoculates to many other herbaceous plants (Gooding, 1962) but does not produce symptoms in sap-inoculated *G. globosa*.

Transmission by Vectors

Literature reports transmission of some viruses that cause diseases of grapevines by leafhoppers, aphids, thrips, mites, scale insects, and by nematodes. The PDV (Pierce's disease virus), also known as alfalfa dwarf (Hewitt, 1953) is spread by many different sharpshooter leafhoppers of the subfamily *Tettigoniellinae* (Delong and Knull as given by Delong and Severin, 1949). The virus is known to have 111 host plants in 41 families, including monocotyledonous and dicotyledonous plants such as herbs, grasses, shrubs and trees (Hewitt, 1953).

Baldacci et al. (1961) report that virus transmitted by sap inoculation from grapevines to herbaceous plants was transmitted from herbaceous plant to herbaceous plant by the aphid, *Myzus persiceae*.

According to Blattný et al. (1956), Melnik mosaic is transmitted by larvae of the soft scale, *Eulacenium corni*.

Ochs (1958a, b, 1960b and c) reports transmission of a number of grape viruses by a number of insect vectors and by nematodes but fails to present reliable experimental evidence to support the reports (Hopp, 1961).

It has been shown that the fanleaf virus of grapevines is soil-borne, and that the dagger nematode, *Xiphinema index,* is the soil-borne vector of this virus (Hewitt, Raski, and Goheen, 1958). Cadman et al. (1960) report that in Portugal the urticado disease of grape often occurs in patches. Soil samples obtained from such patches in two different vineyards showed the distribution of urticado coincided with the presence of a nematode probably identical with *X. index.* Goheen and Hewitt (1962) show that the vein banding disease of grapevines is also soil-borne, and that transmission is associated with the presence of *X. index.*

In California, tests show that the fanleaf virus is not soil-borne in vineyard soils free of *X. index.* In August, 1958, soil samples were taken from the root zone of 19 different fanleaf-diseased vines in a vineyard in Tulare County.

These samples were returned to Davis in 3-gallon nursery cans and planted with healthy St. George rootings. Wet screenings of samples from these soils were examined and the following nematodes found: *X. americanum, Paratylenchus* sp., *Criconemoides* sp., and larvae of *Meloidogyne* sp. After 3 years, none of the vines in these test cans of soil showed symptoms of fanleaf or any other virus disease. This, and the fact that there was no apparent spread of the disease in the vineyard, is evidence that the fanleaf disease does not spread in the absence of *X. index.*

Nematode Transmission of GFV from Herbaceous Plants to Grapevines

In June, 1960, clay pots of steam-pasteurized soil were planted, five with rootings of *V. rupestris* var. St. George, 19 with seedlings of *Chenopodium amaranticolor,* 19 with *Gomphrena globosa,* and five with *C. amaranticolor* and St. George. After the herbaceous plants had reached about the fifth-leaf stage, 14 of the plants of each species were mechanically sap-inoculated with GFV from *G. globosa.* (The GFV was first sap-transmitted to *G. globosa* from St. George.) After 17 days all sap inoculated plants showed virus symptoms. About 200 nonvirus *X. index,* wet-screened from soil around healthy grape roots and suspended in water, were introduced into the root zone of each of seven of the virus-diseased (previously sap-inoculated) *C. amaranticolor* and seven *G. globosa* potted plants. In addition, about 200 *X. index* from the same lot were introduced into the root zone of each of the following control plantings: five healthy St. George rootings; five pots containing one healthy *C. amaranticolor* and one healthy St. George; five pots containing one healthy *G. globosa* and one healthy St. George. After two weeks the seven each of the virus-diseased *C. amaranticolor* and *G. globosa,* were planted each with a healthy St. George rooting. The other seven of the virus-diseased *C. amaranticolor* and *G. globosa* previously infested with *X. index* were planted each with a healthy St. George rooting. Experimental plants tally up as follows:

> 5 pots St. George + *X. index.*
> 5 pots *C. amaranticolor* + *X. index* + St. George
> 7 pots *C. amaranticolor,* GFV + St. George
> 7 pots *C. amaranticolor,* GFV + *X. index* + St. George
> 5 pots *G. globosa* + *X. index* + St. George
> 7 pots *G. globosa,* GFV + St. George
> 7 pots *G. globosa,* GFV + *X. index* + St. George

Early in 1961, the herbaceous plants had all died, and the St. George were forced in the greenhouse. On March 10, there were five of the seven St. George test plants in the series, *C. amaranticolor,* GFV + X. index + St. George, that showed symptoms of fanleaf disease; all other St. George were healthy.

The dagger nematode, *X. index,* moved the GFV from fanleaf-diseased *C. amaranticolor* to St. George but did not move the virus from diseased *G. globosa* to grape. Either the nematodes did not feed on the *G. globosa* or they did not pick up virus from them.

Nematode Transmission of Virus Causing Yellow Mosaic

V i r u s   i s   s o i l - b o r n e. In the spring of 1958, soil was dug from the root zone of 16 different yellow mosaic diseased grapevines in five widely separated vineyards and taken to Davis. Each sample was planted with healthy rootings of the varieties St. George, Carignane, Emperor and Mission.

The following spring, 1959, test plants in three different soil samples had yellow mosaic, the rest were symptomless. By June 1961, test plants in soil from six of the original 16 vines had typical yellow mosaic, two had symptoms of fanleaf and yellow mosaic, one had symtoms of both fanleaf and vein banding, three had symptoms of fanleaf alone, and four test plants remained healthy.

These tests demonstrate the soil-borne nature of the virus which causes yellow mosaic. They also show that the virus which causes fanleaf and that which causes the vein banding disease of grapevines were also transmitted to grape in these soils.

T r a n s m i t t e d   b y   h a n d - p i c k e d   n e m a t o d e s. In the spring of 1959, soil from the three nursery cans referred to above in which the test plants first showed yellow mosaic was wet-screened through 40- and 325-mesh screens. Several species of nematodes, including *X. index* and *C. xenoplax,* were retained on the fine screen. Individual *X. index* specimens were hand-picked from the washings retained on the 325-mesh screen into 30 different lots of 20 individuals each and placed in small beakers of water. Each lot of 20 was then poured about the root zone of a small healthy. *V. rupestris* var. St. George rooting which had been grown from a one-bud cutting in steam-pasteurized soil. Ten healthy St. George rootings were not so treated and were held as control plants. By June 1961, 15 of the 30 St. George plants infested with *X. index* showed virus disease symptoms; of these, two showed only yellow mosaic; two showed yellow mosaic and fanleaf; one had yellow mosaic, vein banding, and fleck; five had only fanleaf symptoms; five had only fleck symptoms; 13 had no virus symptoms and were normal; and two were dead. The 10 control plants appeared normal.

Similar tests with *C. xenoplax* from the root zone, and fungi isolated from roots of plants with yellow mosaic, failed to transmit viruses that produced symptoms in St. George.

In the spring of 1959, another experiment was set up to further test transmission of the GYMV by *X. index*. Rootings of *V. vinifera* varieties, Emperor, Valdepenas and Thompson Seedless, with yellow mosaic disease were used as virus source plants. Healthy rootings of Emperor, Valdepenas, Thompson Seedless and St. George were used as indicator plants. There were 15 nursery pots each planted with one yellow mosaic diseased Emperor, one healthy Emperor and one healthy St. George; 15 similarly planted with Thompson Seedless and St. George; and 15 with Valdepenas and St. George. There were also 10 pots each containing one healthy rooting of Emperor, 10 of Thompson Seedless, 10 of Valdepenas, and 10 of St. George.

A water suspension containing 10 to 15 nonvirus *X. index* was placed in the root zone of 10 of each series of 15 pots containing the combination plantings; five of each did not receive *X. index* and were held for a control. Similarly, to test the nonvirus nature of *X. index,* 10 to 15 were placed in the root zone of five of each of the series of pots containing one grape vine rooting. The other

five pots each containing one rooting were retained as control plants without nematodes.

In the spring of 1960, yellow mosaic showed in the St. George test plant in only one of the combination plantings with Thompson Seedless. In the combinations with diseased Valdepenas, one of the test Valdepenas plants had yellow mosaic, St. George in two pots had yellow mosaic, St. George in three pots had yellow mosaic and typical symptoms of fanleaf, St. George in one pot had only line-pattern symptoms of fanleaf, and St. George in the remaining four pots in the series appeared normal. All test plants in the series with infected Emperor rootings appeared normal, as did all of the test plants in the control pots.

These tests show that *X. index* obtained GYMV from Valdepenas and transmitted the virus to St. George and, to a lesser degree, to Valdepenas; and that the nematode vector also obtained the virus from roots of diseased Thompson Seedless and transmitted it to St. George. The fact that there were transmissions to test plants in six of the ten pots with Valdepenas, only one test plant in the series with Thompson Seedless, and none in the series with Emperor suggests that the nematodes fed on roots of some of the vines and not on roots of others, or that they acquired virus from some and not from others. The test shows that *X. index* obtained and transmitted the GFV as well as GYMV from the Valdepenas with yellow mosaic, even though it displayed no symptoms of fanleaf.

Relationships of the Soil-Borne Grape Virus Diseases

Though the soil-borne virus diseases fanleaf, yellow mosaic, and vein banding are distinct, have constant symptoms, and are fairly easily distinguished one from the other, it appears now they may be caused by strains of the same virus. In California, the three diseases are usually associated. Vines with yellow mosaic are usually found in rather distinct, delimited, circular areas that are themselves within a larger area of fanleaf-diseased vines. It is only rarely that we find isolated yellow-mosaic-diseased vines, and when we do they occur somewhat together in a row as if budded from the same bud stick. Most of the yellow mosaic spots in fanleaf-diseased vineyards spread from the margins as does the fanleaf disease. Likewise the vein banding disease is associated with fanleaf and spreads through the soil from the margins like fanleaf and yellow mosaic.

Vines of several different varieties diseased with yellow mosaic and also vein banding are found to have symptoms such as cane malformations, double nodes, et cetera, that overlap those prominently associated with fanleaf. In the past we have considered this to be an indication of the presence of mixtures of viruses forming a disease complex. This may be so, but it could also be an expression of a mixture of strains of the same virus.

A chrome-yellow factor, a color like that in yellow mosaic, is often found in leaves of vines with the fanleaf and vein banding diseases. Many of the California fanleaf strains produce no chrome-yellow color in leaves; these we have considered to be the basic fanleaf strain. Numerous attempts have been made to separate out and identify the virus that induces chrome-yellow color.

Thus far, these efforts have shown chrome-yellow to be an integral part of the selection or isolate of fanleaf, vein banding, or yellow mosaic. Furthermore, the chrome-yellow color is soil-borne along with fanleaf, vein banding, and yellow mosaic.

A collection of vines with the chrome-yellow factor has been organized in a series that shows from little to much yellow in the leaves. Some of the strongly colored forms are separated from yellow mosaic only by the fact that the shoots in the spring are not yellow as are those on a vine with yellow mosaic.

The dagger nematode *X. index* is the vector of the GFV and GYMV. There is evidence indicating that the same nematode is the vector of the virus that causes the vein banding disease (Goheen and Hewitt, 1962).

By mechanical inoculation to herbaceous plants, sap from leaves or roots of yellow mosaic, vein banding and fanleaf-diseased vines each produce symptoms that are mostly indistinguishable one from the other in *C. amaranticolor* and in *G. globosa*.

Other viruses, such as TMV (tobacco mosaic virus), are known to have a wide variety of strains, some without the yellow color factor and some that produce varying degrees of yellow color in host plants (Smith, 1957). This analogy, in addition to the other evidence presented, suggests to us that yellow mosaic, vein banding, and fanleaf, are but strains of the same virus.

The only fact that seems to be in conflict with this is that yellow mosaic spreads in a vineyard even to vines that are fanleaf-diseased. This suggests that the fanleaf virus thus does not cross-protect for the yellow mosaic virus and, therefore, is not a strain of the same virus. There are many factors that apparently influence the degree of protection of a plant infected by one strain against the effects of another (Bawden, 1956). Heavy doses of some virus strains introduced by grafting overcome an effect of cross-protection of others (Bawden, 1956). Mild strains of some viruses will cross-protect for some but will not cross-protect for other strains of a virus (Cochran and Rue, 1946).

Although the yellow vein disease possesses the chrome-yellow factor, it is differentiated from yellow mosaic, fanleaf and vein banding by symptoms on different indicator plants. For example, the Mission variety will show fanleaf, yellow mosaic, and vein banding, but when chip-bud grafted to several selections of yellow vein, Mission indicator plants do not show yellow vein. Also, yellow vein does not produce symptoms in the rootstock varieties St. George or 5 BB. Yellow vein virus will mechanically sap inoculate to a number of herbaceous plants and produce symptoms distinct and different from those produced by inoculations from fanleaf, yellow mosaic, or vein banding (Gooding, 1962). Attempts to transmit this virus by nematodes have failed. Thus, yellow vein appears not to be a strain of the fanleaf virus.

Chemical Treatment of Soil for Control of Soil-Borne Grape Virus Diseases

Ravaz (1930) reported laboratory and field experiments that indicate a measure of control of court noué with carbon bisulfide, formaldehyde and heavy doses of lime. Vuittenez (1957 and 1960b) obtained a very good measure of

control of the soil-borne diseases of grapevines with DD (1,2-dichloropropane and 1,3-dichloropropene) and methyl bromide, and a fair degree of control with carbon bisulfide.

In California field experiments to test chemical control of the soil-borne virus diseases of grapevines were started in Napa Valley, California, in the fall of 1953.

Test plot no. 1. The first plot selected, which we will designate Test No. 1, was a block of Pinot Chardonnay vines on rootstocks of *V. rupestris* var. St. George. All vines in the plot were diseased. They were pulled in September, 1953, and the ground was prepared and treated in early October. The plot was a long rectangle, a little over four acres in area. Soil samples taken before treatment contained nematodes in the genera *Xiphinema* and *Criconemoides*. Treatments were laid out in six equal longitudinal strips. Two strips were not treated, one serving as a control and the other being used to test soil transmission to certain rootstocks under field conditions. Chemicals were applied to each of the other four strips, respectively, at the following rates per acre: CS_2 (carbon bisulfide), 3200 lbs; D. D. (1,3-dichloropropene and other chlorinated hydrocarbons), 800 lbs; CBP (chlorobromopropane), 40 gallons; and EDB (ethylene dibromide), 30 gallons. The entire rectangular plot was divided horizontally at the center; the halves were designated replications 1 and 2. Replication 1 was a clay loam with sand and gravel; replication 2 was more sandy, with and under

Table 1

Test plot no. 1: The total number of fanleaf diseased vines in the fall of 1957 in soil chemical treatment plots planted in 1954, 1955 and 1956, respectively, 6, 18 and 30 months after treatment

Treatments in 1953	Total number of vines per replication	Date of planting and replication					
		1954 Replication		1955 Replication		1956 Replication	
		1	2	1	2	1	2
Control — no treatment	50	43	39	8	20	5	6
Rootstocks — no treatment 1202	20	4*)	8	3	12	1	2
AXR / 1	20	10	11	4	4	7	0
99 R	10	2*)	3*)	1	2	6	1
Ethylene dibromide	40	28	21	10	6	2	2
Chlorobromopropane	40	26	14	4	6	3	5
D.D.	40	20	7	1	8	5	3
CS_2	40	1	6	—	—	—	—

*) Many of the rootstock vines died the first year

layer of gravel at about four feet. One fourth of each replication was planted in April, 1954, one fourth of each replication of each treatment excepting CS$_2$ was planted in 1955, and also another one fourth in 1956, that is, respectively, 6, 18,

Table 2

Test plot no. 1: The number of new cases of fanleaf showing in replicated soil treatment plots each of three successive years following plantings in soil that was treated in the fall of 1953 and planted in the spring of 1954

Treatments	Replication 1			Replication 2		
	1955	1956	1957	1955	1956	1957
Control	11	8	24	15	10	14
Ethylene dibromide	5	0	23	2	0	19
Chlorobromopropane	0	2	24	0	2	12
D.D.	2	4	14	0	2	5
CS$_2$	1	2	3	0	0	1

Table 3

Test plot no. 2: Results of chemical application to control soil-borne grape viruses. Data obtained 3 years after treatment and planting

Treatment	Rate of application	No. diseased to healthy	Mean angle*)	Average percentage*)
Check		30/33	79.6	96.8
Chloropicrin	1 lb per 100 sq ft	33/48	59.5	74.2
D.D.	40 gal per acre	20/40	49.4	57.6
CS$_2$	8.34 lb per 100 sq ft	22/40	48.4	56.0
Nemagon	5 gal per acre	20/39	44.6	49.4
Ethylene dibromide	15 gal per acre	18/42	35.5	33.7
Methyl bromide	1 lb per 100 sq ft	10/41	24.9	17.7
Methyl bromide	2 lb per 100 sq ft	7/52	18.9	10.5
Methyl bromide	4 lb per 100 sq ft	5/42	14.9	6.6
LSD 5 %			24.6	
1 %			33.0	

*) Based on transformation of percentages to angles and angles to percentages as given by SNEDECOR (1946) p. 449-450

and 30 months after treating the soil. The remaining areas were not planted. The plot was destroyed in the fall of 1957. Results of the treatments are given in Table 1, which shows the number of diseased vines in each replication at 4, 3 and 2 seasons after planting.

It is evident the soil treatments did not eliminate soil-borne virus from the soil. The plot treated with CS_2, however, had fewer virus-diseased vines than did any of the other plots. The rate of recurrence of diseased vines, as shown for the 1954 planting in Table 2, is perhaps a qualitative measure of the relative effectiveness of the different chemicals. It was not until the third year after treating and planting that there was a marked increase in diseased vines in the chemical treatments, whereas the number of newly diseased vines in the control plot was fairly high each year. Vines in the plots showed typical fanleaf and vein banding, with and without a chrome-yellow factor.

Test plot no. 2. Various chemical soil treatments were applied to plots on the Federal experiment station grounds in Fresno County, California, in April 1956, a few weeks after a block of virus-diseased vines had been removed. Each treatment plot was 10×20 feet. They were randomized by lot in each of five replications. The treatments and rates of application are shown in Table 3.

In May 1956, the plots were planted; 10 rootings each of healthy Mission and French Colombard were lined out through the center of each plot. In April 1957, the places where Mission and French Colombard vines had died were replanted with healthy St. George rootings. The varieties are all good indicators of the soil-borne grape viruses. Table 3 shows the ratio of diseased to healthy plants three years after treatment.

Percentage data were transformed to angles with BLISS's transformation as given by SNEDECOR (1946) for analyses of variance, and averagen percentages (in the column at the right of Table 3) were obtained from mean angles. Methyl bromide at 4 lbs per 100 sq ft was the best treatment. At the 5 % level, all treatments were better than the control.

Table 4

Test plot no. 3: The number of fanleaf-diseased vines in different treatments two seasons after planting in soil plots that were treated 24 months after removing the old diseased vineyard

Plot treatment	Total vines in plot	Fanleaf-diseased vines	
		No.	%
Control — no treatment	304	73	24.3
200 lb methyl bromide/acre	304	49	16.4
400 lb methyl bromide/acre	304	17	5.6
3200 lb carbon disulfide/acre	298	7	2.3

T e s t   p l o t   n o. 3. In the fall of 1957, another 4-acre vineyard of Pinot Chardonney on St. George rootstock in Napa Valley was pulled. All vines in the vineyard had fanleaf, vein banding, chrome-yellow flecked leaves, or a combination of the three disease symptom patterns. The plot was winter-cropped to barley and summer-fallowed during 1957 — 58 and 1958 — 59. In September 1959, the 4-acre rectangle was divided into four equal strips. One strip was left untreated as a control, a second strip was treated with CS_2 at 3200 lbs per acre, and the remaining strips treated with methyl bromide at rates of 200 and 400 lbs per acre, respectively. The entire plot was planted with healthy St. George rootstocks in the spring of 1960 and chip-bud grafted to Pinot Chardonnay in August. The vines were trained on stakes in 1961. By August 24, 1961, virus diseased plants had developed in all plots: 24.3 per cent in the control, 16.4 per cent and 5.6 per cent, respectively, in the 200 lb and 400 lb methyl bromide plots, and 2.3 per cent in the soil treated with CS_2 (Table 4).

Eradication of the dagger nematode vector of these soil-borne viruses appears, from the results of the different treatments, to be difficult.

The presence of nematodes in the plot was determined from 400-gram soil samples taken at interval depths of 1, 2, 3, and 4 feet at each of four stations in each treatment strip; at some stations samples were taken to a depth of eight feet. Samples were wet-screened and the number of *X. index* in each counted. Table 5 shows the total number of nematodes, adults and larvae, found in each sample taken in the spring of 1960 seven months after soil treatments, and again in the spring of 1961. These samples show that the nematodes survived in all treatments, that they were irregularly distributed in the soil, and that they occurred at least to depths of eight feet. From samples in other vineyards it has been determined that this nematode occurs at much greater depths.

C o n t r o l   o f   d i s e a s e s. Control of the plant viruses that are biologically soil-borne requires that the cycle of virus to vector be broken. In the event that the virus is persistent in the vector, it would be necessary to destroy the vector; but if the virus were nonpersistent in the vector it would be necessary only to destroy the source or reservoir of virus.

Raski and Hewitt (1960) showed that *X. index* held in moist soil, free of living plant roots, retained the fanleaf virus for only about 30 days. Later work by Raski and Hewitt (1961) shows that nematodes may retain the GFV up to 120 days. The fanleaf virus will, it appears, eventually disappear from the dagger nematodes provided they do not again feed on a root with virus. It should be possible then to control soil-borne fanleaf in old vineyard soils by destroying the soil reservoir of virus.

If the perennial roots left in the soil after removing the vines are the source of the fanleaf virus, then the destruction of the roots should break the virus-vector relationship. The destruction of all living roots is an enormous task because the grapevine roots are deep and live a long time after the top is removed, possibly for several years. We have dug living roots from soil three years after removing vines. Root destruction can be hastened, perhaps, by destroying the tops of plants at a time when the carbohydrates in the roots are low. Winkler and Williams (1945) show that the roots of grapevines are low in stored carbohydrates from June through August. If the vines to be destroyed were girdled during this period to prevent movement of carbohydrates to the roots, it is

Table 5

Chemical control test plot no. 3: The number of dagger nematodes in 400-gram soil samples from different depths at stations in the different treatments 7 and 19 months after treatment

Plot treatment	Depth of sample in feet	Number of dagger nematodes							
		Stations 1960				Stations 1961			
		1	2	3	4	1	2	3	4
Control —	1	0	0	0	0	1	0	0	0
no treatment	2	2	2	0	0	0	0	0	3
	3	20	1	–	1	13	1	–	0
	4	12	0	–	0	3	0	–	1
Methyl bromide	1	0	0	0	0	0	0	0	0
at 200 lb/acre	2	0	1	0	0	0	2	3	1
	3	0	0	0	0	0	0	4	3
	4	2	1	3	1	5	0	0	5
Methyl bromide	1	0	0	0	0	0	0	7	0
at 400 lb/acre	2	0	0	0	0	0	0	4	0
	3	0	0	0	0	0	0	0	0
	4	0	0	1	1	0	0	0	2
	5	2	–	0	13	0	–	2	9
	6	1	–	0	21	1	–	7	1
	7	0	–	31	135	0	–	13	2
	8	1	–	5	57	1	–	3	2
Carbon bisulfide	1	0	0	0	0	0	0	0	0
at 3200 lb/acre	2	0	0	1	0	0	0	2	0
	3	0	0	2	0	0	0	3	0
	4	0	0	6	0	0	0	7	1

probable that the roots would use up the remaining supply sooner than in nongirdled vines and thus be more susceptible to decay. A fairly weak herbicide applied to the vines 10 days before girdling should increase root activity and thus also contribute indirectly to hasten root decay.

Roots of some herbs may also serve as a source of GFV. We have shown that X. index will acquire the virus from roots of C. amaranticolor and subsequently transmit the GFV to grapevine through the roots. X. index could carry over the virus from one crop of seed plants to another, because vineyard soils in California are not usually free of weed plants for more than 120 days. It is also probable that the virus could be carried over from one crop of weeds to another through the seeds, for BRÜCKBAUER and RÜDEL (1961b) have shown the GFV to be seed-borne in C. amaranticolor.

To obtain control of soil-borne fanleaf by the destruction of the virus reservoir, it appears that it would be necessary to hold the land until all roots had died.

Summary

The principal symptoms that characterize the virus diseases of grapevines found in vineyards of California are described. The diseases are: Pierce's disease, fanleaf, yellow mosaic, vein banding, leafroll, yellow vein, asteroid mosaic, and corky bark. It is the first report of the graft transmission of corky bark and an unidentified virus that produces fleck in *Vitis ruprestris* var. St. George.

All of the grape viruses can be transmitted by one or more grafting methods, but chip-bud grafting has proved to be simple and effective. The soil-borne viruses that cause fanleaf, yellow mosaic, and vein banding all mechanically sap-transmit to, and produce very similar, mostly indistinguishable symptoms in different herbaceous hosts. The GYVV (grape yellow vein virus) will also sap-transmit to several different herbs, yet the symptoms differ from those induced by the soil-borne viruses.

Xiphinema index transmitted the GFV (grape fanleaf virus) from roots of sap-inoculated *Chenopodium amaranticolor* to roots of *V. rupestris* var. St. George. Evidence shows that *X. index* will also transmit the GYMV (grape yellow mosaic virus) from vine to vine.

Evidence indicates that fanleaf, yellow mosaic, and vein banding are distinct diseases with definite and consistent symptoms, although apparently caused by strains of the same virus.

Results of these tests to control the soil-borne grape viruses by injection of chemicals into the soil show that carbon bisulfide and methyl bromide are the most effective, though none of the chemicals used give complete control.

Literature Cited

Amici, Adriana, E. Baldacci and E. Refatti: In Merito alla utelizazione di piante test erbacee nella diagnosi della virosi della vite (degenerazione infettiva) per inoculazione meccanica. Ann. Fac. Agr. Milano, NS, 7, 41 — 48 (1958).

Baldaccí, E., Adriana Amici, L. Bonola, E. Betto, G. Fogliani and E. Refatti: Transmissione su piante erbacce della virosi della vite nota come "degenerazione infettiva." Ricerca Sci. 30, 981 — 983 (1960).

— — , — — , G. Belli, E. Betto, P. Bonola, G. Fogliani, G. Giussani and E. Refatti: Ricerche sulle malattie da virus della vite: semeiotica, eziologia, perpetuazione e prevenzione. Riv. patol. vegetale, Ser. III, 1, 113 — 231 (1961).

Bawden, F. C.: Plant viruses and virus diseases. Third Ed. Chronica Botanica Co., Waltham, Mass., USA, 335 p. (1956).

Blattný, C., B. Starý and J. Nedomlel: Choroby a škůdci ovocných rostlin. Nakladatelství Českolov. Aka. Věd., Praha, 534 p. (1956).

Bovey, R.: Etat actuel des connaissances sur les maladies à virus de la vigne. Vitis 1, 237 — 256 (1958).

Brückbauer, H.: Untersuchungen zur Frage der Übertragbarkeit der Reisigkrankheit der Rebe durch Pfropfung. Mitt. Klosterneuburg 7A, 171 — 188 (1957).

— — and M. Rüdel: Untersuchungen über die Viruskrankheiten der Rebe. II. Mechanische Übertragung der Reisigkrankheit auf krautige Testpflanzen. Wein Wiss. **16**, 113 — 134 (1961a).

— — and — — : Untersuchungen über die Viruskrankheiten der Rebe. III. Samenübertragbarkeit der Reisigkrankheit des Silvaners bei einer Testpflanze sowie Untersuchungen über das evtl. Vorkommen des Virus in Weinbergsunkräutern. Wein Wiss. **16**, 187 — 189 (1961b).

— — and — — : Untersuchungen über die Viruskrankheiten der Rebe. IV. Weitere Untersuchungen zur mechanischen Übertragung der Reisigkrankheit auf krautige Testpflanzen. Wein Wiss. **16**, 206 — 217 (1961c).

Cadman, C. H., H. F. Dias and B. D. Harrison: Sap-transmissible viruses associated with diseases of grape vines in Europe and North America. Nature (London) **187**, 577 — 579 (1960).

Caudwell, A.: Deux années d'études sur la flavescence dorée nouvelle maladie grave de la vigne. Ann. Amélior. Plantes. **4**, 359 — 393 (1957).

Ciccarone, A.: La degenerazione infettiva ed altre alterazione della vite. Ital. Agr. **98**, 887 — 921 (1961).

Ciferri, R., A. Corte and G. Scaramuzzi: Suscettibilitâ di piante arboree alla sindrome virosica della "degenerazione infettiva" della vite. Atti. Ist. botan. univ. Lab. crittogam., Pavia., Ser 5, **16**, 335 — 352 (1959).

Cochran, L. C. and J. L. Rue: Interaction of some forms of the peach-mosaic virus. (Abstr.) Phytopathology **36**, 396 (1946).

Cook, J. A. and A. C. Goheen: The effects of a virus disease, leafroll, on the mineral composition of grape tissue and a comparison of leafroll and potassium deficiency symptoms. Amer. Inst. Biol. Sci. Publ. No. 8, 338 — 354 (1961).

Delong, D. M. and H. H. P. Severin: Characters, distribution and food plants of leafhopper vectors of virus causing Pierce's disease of grapevines. Hilgardia **19**, 171 — 186 (1949).

Dias, H. F.: O "nó-curto infeccioso" da videira (urticado). Thirteenth Congr. Luso-Espanhol Prog. Ciencias, 5, 167 — 175 (1950a).

: "Clorose infecciosa" da videira (panachure ou mosaico branco). Thirteenth Congr. Luso-Espanhol Prog. Ciencias, 5, 177 — 182 (1950b).

— — : Alguns ensaios sobre o "nó-curto" (urticado) e a "clorose infecciosa" da videira. Thirteenth Congr. Luso-Espanhol Prog. Ciencias, 5, 183 — 187 (1950c).

— — : Clorose infecciosa da videira. I Expressão simtomatológica da "virose" nos principais porta-enxertos. Agronomia lusitana **17**, 367 — 374 (1955).

du Plessis, S. J.: Virus diseases and some symptomologically related abnormalities of the vine. Ann. Univ. of Stellenbosch. 26A, 1 — 33 (1950).

Ehrenhardt, H. and H. Brückbauer: Das Problem der Rebvirosen. Entgegnungen und Fragen zu den Arbeiten von Ochs. Weinberg u. Keller 5, 621 — 630 (1959).

Gärtel, W.: Panaschüren bei Reben. Weinberg u. Keller **1**, 137 — 145 (1954).

— — : Die "flavescence dorée" oder "maladie du Baco 22A." Weinberg u. Keller 6, 295 — 311 (1959).

Gifford, E. M., Jr., Wm. B. Hewitt, A. D. Graham and C. H. Lamoureux: An internal symptom for identifying fanleaf in the grapevine. Calif. Dep. Agr. Bull. **45**, 368 — 372 (1956).

Goheen, A. C. and J. A. Cook: Leafroll (red-leaf or rougeau) and its effects on vine growth, fruit quality, and yields. Amer. Jour. Enol. and Vit. **10**, 173 — 181 (1959).

— — , F. N. Harmon and J. H. Weinberger: Leafroll (white Emperor disease) of grapes in California. Phytopathology **48**, 51 — 54 (1958).

— — and Wm. B. Hewitt: Vein Banding, a new virus disease of grapevines. Amer. Jour. Enol. and Vit. **13**, 73 — 77 (1962).

— — , — — and C. J. Alley: Studies of grape leafroll in California. Amer. Jour. Enol. and Vit. **10**, 78 — 84 (1959).

— — and W. C. Schnathorst: Resistance to powdery mildew in leafroll-affected grapevines. Plant Disease Rep. **45**, 641 — 643 (1961).

Gooding, Guy V., Jr.: The grape yellow vein disease and characterization of the causal virus. Ph. D. Thesis, Grad. Div., University of California. (1962).

Graniti, A.: Probabile presenza della "malattia delle enazione" della vite in Puglia. Notiz. malattie piante, NS, **26-27**, 140 — 143. (In R.A.M. **38**, 648) (1959).

Harmon, F. N. and E. Snyder: Investigations of the occurrence, transmission, spread, and effect of "white" fruit color in the Emperor grape. Proc. Amer. Soc. hort. Sci. **47**, 190 — 194 (1946).

Hewitt, Wm. B.: A graft-transmissible mosaic disease of grapevine. Phytopathology **35**, 940 — 942 (1945).

— — : Fanleaf-another vine disease found in California. Calif. Dep. Agr. Bull. **39**, 62 — 63 (1950).

— — : Virus diseases of grapevines, pp. 744 — 753. In U. S. Dept. Agric. Plant Diseases, the Yb. Agric. Washington D.C. (1953).

— — : Some virus and virus-like deseases of grapevines. Calif. Dep. Agr. Bull. **43**, 47 — 64 (1954).

— — : Yellow vein, a disease of grapevines caused by a graft-transmissible agent. (Abstr.) Phytopathology **46**, 15 (1956).

— — : The probable home of Pierce's disease virus. Plant Disease Rep. **42**, 211 –- 215 (1958).

— — and C. J. Delp: Yellow mosaic of grapevines and evidence of retention of the virus in the soil. (Abstr.) Phytopathology **43**, 475 (1953).

— — and E. M. Gifford, Jr.: Symptoms for identifying fanleaf in dormant grapevines. Calif. Dep. Agr. Bull. **45**, 249 — 252 (1956).

— — and A. C. Goheen: Asteroid mosaic of grapevines in California. (Abstr.) Phytopathology **49**, 541 (1959).

— — , D. J. Raski and A. C. Goheen: Nematode vector of soil-borne fanleaf virus of grapevines. Phytopathology **48**, 586 — 595 (1958).

Hopp, H. H.: Zum Stand der Übertragbarkeit von Rebvirosen. Weinberg u. Keller **6**, 9 — 17 (1959a).

— — : Überprüfung und Variation einer Methode zum Nachweis und zur Identifizierung von Rebviren. Jahresber. 1958 des Staatl. Weinbauinst. Freiburg/Br., 17 (1959b).

— — : Bemerkungen zu drei 1960/61 erschienenen Veröffentlichungen von G. Ochs. Weinberg u. Keller **8**, 83 — 86 (1961).

Niemeyer, L. and O. Bode: Über den Virusnachweis bei Reben. (Bemerkungen zu einer Veröffentlichung von G. Ochs). Z. Pfl.-Krankh. **66**, 640 — 644 {1959).

Ochs, G.: Der heutige Stand der Reisigkrankheitsforschung. Angew. Bot. **29**, 152 — 159 (1955).

— — : Ein Virustest für Reben. Mitt. Klosterneuburg **7A**, 274 — 278 (1957).

: Über drei Viren als Erreger von Rebkrankheiten. Z. Pfl.-Krankh. **65**, 11 –- 17 (1958a).

: Untersuchungen über die Verbreitung der Rebenviren durch Vektoren. Naturwiss. **45**, 193 (1958b).

— — : Wie verhalten sich Unkräuter und Nutzpflanzen im Weinberg zum Panaschürevirus der Rebe? Rebe u. Wein **11**, 183 — 184 (1958c).

— — : Mechanische Übertragung der drei Rebvirosen, infektiöse Panaschüre, Blattdeformation und Jaune canare. Mitt. Klosterneuburg. **10A**, 53 — 56 (1960a).

— — : Gelungene Übertragungsversuche von Viruskrankheiten der Rebe durch Nematoden. Mitt. Klosterneuburg. **10A**, 97 — 101 (1960b).

— — : Übertragungsversuche von drei Rebviren durch Milben und Insekten. Z. Angew. Zool. **47**, 485 — 491 (1960c).

— — : Die kanariengelbe Verfärbung der Rebe. Rebe u. Wein **12**, 195 — 196, 198 (1960d).

Petri, L.: Sulle cause dell'arricciamento della vite. Boll. regia Staz. patol. vegetale, NS, **9**, 101 — 130 (1929).

Raski, D. J. and Wm. B. Hewitt: Experiments with *Xiphinema index* as a vector of fanleaf of grapevines. Nematologica **5**, 166 — 170 (1960).

— — and — — : Plant-parasitic nematodes as vectors of plant viruses. Symp. on Inter-relationships between nematodes and other agents causing plant diseases. 53rd Ann. Meeting Amer. Phytopath. Soc., Biloxi, Miss. (To be published in Phytopathology). (1961).

RAVAZ, L.: Sur le court-noué. Ann. école nat. agr. Montpellier, NS, **20**, 110 — 125 (1930).

SCHEU, G.: Mein Winzerbuch. Reichsnährstands-Verlag. Berlin, 274 p. (1936).

SMITH, K. M.: A textbook of plant virus diseases. Second Ed. Little, Brown and Company, Boston, 652 p (1957).

SNEDECOR, G. W.: Statistical methods. Fourth Ed. Iowa State College Press, Ames, 485 p. (1946).

STRANAK, F., C. BLATTNÝ and A. KLEČKA: Mosaika Reby vinne (Přdběžné Sdělení). Ochrana Rostlin **11**,·89 — 98 (1931).

VUITTENEZ, A.: Transmission par double greffage d'une panachure infectieuse de la vigne. C. R. Acad Sci. (Paris) **234**, 1084 — 1086 (1952).

— — : Variation des symptômes de la dégénérescence infectieuse de la vigne. Interprétation d'expériences de transmission de la maladie par greffage. C. R. Acad. Sci. (Paris) **243**, 515 — 517 (1956).

: Lutte préventive contre le court-noué de la vigne par la désinfection chimique du sol avant la plantation. C. R. Acad. agr. France **43**, 185 — 196 (1957).

— — : Mise en évidence chez les vignes atteintes de dégénérescence infectieuse, d'un virus transmissible mécaniquement aux Chénopodes *(Chenopodium amaranticolor* et *C. quinoa)*. C. R. Acad. Sci. (Paris) **251**, 783 — 785 (1960a).

— — : Nouvelles observations sur l'activité des traitements chimiques du sol pour l'éradication des virus de la dégénérescence infectieuse de la vigne. C. R. Acad. agr. France **20**, 89 — 99 (1960b).

WILHELM, A. F.: Panaschüre, eine Viruskrankheit im Weinbau. Dtsch. Weinbau **1**, 8 — 10 (1955).

WINKLER, A. J. and W. O. WILLIAMS: Starch and sugars of Vitis vinifera. Plant Physiology **20**, 412 — 432 (1945).

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