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# SUGAR-BEET MOSAIC

HENRY H. P. SEVERIN
and
ROGER M. DRAKE

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

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H I L G A R D I A

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# SUGAR-BEET MOSAIC[1]

**HENRY H. P. SEVERIN[2] and ROGER M. DRAKE[3]**

## SUMMARY

Sugar-beet mosaic investigations conducted in California include tests on host range, symptomatology, properties of the virus, and various aspects of transmission by insects, especially aphids.

The economic plants in one family demonstrated to be naturally infected with the sugar-beet-mosaic virus were as follows:

Chenopodiaceae:
*Beta vulgaris,* sugar beet, mangel or stock beet, and garden beet
*Beta vulgaris* var. *cicla,* Swiss chard
*Spinacia oleraceae,* spinach

In addition to the economic plants naturally infected, the following plants in three families were experimentally infected with the virus:

Chenopodiaceae:
*Kochia scoparia* var. *trichophila,* common summer cypress
Aizoaceae:
*Tetragonia expansa,* New Zealand spinach
Solanaceae:
*Nicotiana tabacum,* tobacco (Havana-type variety and Primus variety)

The sequence of symptoms on these host plants, and even on a single host plant, vary widely. The incubation period of the disease in sugar beets averages about 8 days in the greenhouse and 25 days outdoors.

Ten species of plants in five families were found to be nonsusceptible. An attempt was made to recover the virus from all plants that failed to show symptoms.

The properties of the virus extract from the leaves are summarized as follows: thermal inactivation was 60° C in 10-minute exposures; freezing the expressed juice at −18° C resulted in a monthly decrease in the number of infections to zero at the end of five months; tolerance to dilution of extracted juice was 1:5,000; and tolerance to aging *in vitro* at room temperature was 6 days.

[1] Received for publication December 13, 1947.
[2] Entomologist in the Experiment Station.
[3] Formerly graduate student in Entomology and Parasitology.

No transmission was obtained with eight species of insects other than aphids.

The following four aphid species which multiplied on sugar beets transmitted the virus: erigeron root aphid, *Aphis middletonii* (Thomas); bean or dock aphid, *A. rumicis* Linnaeus; pea aphid, *Macrosiphum pisi* (Kaltenbach); and green peach aphid, *Myzus persicae* (Sulzer).

The following eleven aphid species reared on other host plants are vectors of the virus: celery leaf aphid, *Aphis apigraveolens* Essig; celery aphid, *A. apii* Theobald; rusty-banded aphid, *A. ferruginea-striata* Essig; cotton or melon aphid, *A. gossypii* Glover; bur clover or cowpea aphid, *A. medicaginis* Koch; green apple aphid, *A. pomi* De Geer; cabbage aphid, *Brevicoryne brassicae* (Linnaeus); yellow willow aphid, *Cavariella capreae* (Fabricius); foxglove aphid, *Myzus solani* (Kaltenbach); honeysuckle aphid, *Rhopalosiphum conii* (Davidson); and turnip or false cabbage aphid, *R. pseudobrassicae* (Davis).

A summary of the percentages of infections obtained with all aphid species is given in table 8 (page 513).

Virus transmission by lots of 20 *Aphis middletonii, Macrosiphum pisi,* and *Myzus persicae* reared on mosaic beets was compared with that by mechanical inoculation. Infections obtained with the three aphid species were 20, 60, and 56 per cent, respectively, as compared with 96 per cent by mechanical inoculation of the virus extract from the plants on which they were reared. The transmission of the virus by ten aphid species reared on other host plants varied from 8 to 76 per cent, as compared with 88 to 100 per cent by mechanical inoculation of juice expressed from the same mosaic beets on which the aphids were forced to feed.

With *Myzus persicae,* the percentages of infections produced increased with the number of aphids per plant.

Short feeding time of winged aphids on mosaic and healthy beets may be of significance in the natural spread of the disease, since lots of 1, 2, 3, 4, and 5 green peach aphids gave infections averaging 0, 25, 25, 40, and 45 per cent, respectively, after having fed 5 minutes on mosaic and 5 minutes on healthy beets.

The retention of the virus by lots of 20 infective aphids varied from 1 to 3 hours under greenhouse conditions.

In one instance, aphids recovered the virus from a sugar beet infected with the virus 1 day before symptoms of the disease developed, in another instance on the same day after the first symptom appeared, and in others 1 to 2 days after the earliest symptom developed.

No infections were obtained by inoculating the cornicle exudate from infective aphids into healthy beet seedlings.

Multiple viruses in a sugar beet were separated by previously noninfective *Myzus persicae,* which recovered the sugar-beet-mosaic virus, and by previously noninfective beet leafhoppers (*Eutettix tenellus*), which recovered the curly-top virus.

## INTRODUCTION

Sugar-beet mosaic is not a killing virus of sugar beets, mangels, or garden beets, and has nowhere proved to be important in commercial fields in California. During the spring of 1927, the green peach aphid, *Myzus persicae* (Sulzer), was extremely abundant on the plains and foothills in the middle

San Joaquin Valley and destroyed most of the pasture vegetation during March on the plains and foothills. After the pasture vegetation began to wilt, enormous flights of aphids occurred into the cultivated areas. That year most of the sugar beets showed symptoms of beet mosaic. Small beets were temporarily stunted, but as the season advanced, they recovered and produced a marketable crop. No information is at hand on the reduction in yield and sugar content.

On the other hand, in sugar and garden beets grown for seed, mosaic is a serious disease in California: when the stecklings or mother beets are infected before transplanting, considerable reduction in seed yield results.

An enormous amount of literature has been published on this disease in Europe and America. Papers that concern the aspects of the disease that were included in this investigation are reviewed in the following section.

An investigation was undertaken on naturally and experimentally infected host plants of sugar-beet mosaic and the sequence of symptoms was studied. Experiments were conducted to determine some of the properties of the virus. Attempts were made to transmit the virus with insects exclusive of the Aphididae, and also with aphid species that were reared on sugar beets and on other host plants. Aphids were compared with mechanical inoculation as a means of transmitting the virus. Other aspects of aphid transmission of the virus of sugar-beet mosaic discussed in this paper, include a comparison of the transmission of the virus by varying numbers of aphids, the transmission of the virus in short feeding time, the retention of the virus by aphids, and loss and recovery of the infectivity by aphids on inoculated plants. An attempt was made to separate multiple viruses in a sugar beet.

## REVIEW OF LITERATURE

**Common Names and Symptoms of the Disease.** The first mention of this disease has been credited to Prillieux and Delacroix (1898),[4] who called it "jaunisse," or yellows. They give the following sequence of symptoms: At first the leaves lose their normal turgescence, the petioles become less rigid, and the tip of the leaf turns down. At the same time the leaves become finely variegated, green and white. With the progress of the disease, the discolored spots coalesce; at this time the color varies from yellow to gray and the leaf becomes dry. When the plants are severely affected, the beet roots do not increase in size, although they retain their normal sugar content.

The diseases called "jaunisse" by Prillieux and Delacroix (1898) and "gulsot" by Rostrup (1904) and Eriksson (1912) are described as beginning with a slight wilting. As Quanjer (1936) points out, this is not a symptom of sugar-beet mosaic; but he infers from the later symptoms—yellowing of the full-grown leaves and mottling of the heart leaves—that both virus yellows and mosaic must have been present.

The mottling and the fusion of the discolored spots are symptoms of a beet mosaic, but all other symptoms described are not typical of the disease as it occurs in California.

Townsend (1915) suggested the name "sugar beet mosaic" when he described the symptoms of the disease on sugar beets in the United States, and stated that it was observed more than a dozen years before its publication.

[4] See "Literature Cited" for citations, referred to in the text by author and date.

**The Question of Multiple Viruses.** The question of whether or not the symptoms described for beet mosaic are caused by a single virus or by multiple viruses in the same plant has been disputed by several investigators. Quanjer (1936) is of the opinion that a virus complex of mosaic and a disease of the type of virus yellows occurs in North America. This opinion is based on his contention that, contrary to Robbins (1921) and Verplancke (1934), phloem necrosis and starch accumulation are associated not with mosaic, but with virus yellows. He likewise asserts that the disease called "jaunisse" by Prillieux and Delacroix (1898) in France, and "gulsot" by Rostrup (1904) and Eriksson (1912) in Sweden, and "sugar-beet mosaic" by Townsend (1915) in the United States is a mixture of the two viruses; and that the mosaic disease investigated by Brandenburg (1927) and Böning (1927*a*) in Germany was not free from virus yellows in its later stages.

In another paper, Böning (1927*b*) used the terms "stipple, spot, point, net, and mosaic" to describe different types of the disease; but whether these are caused by different viruses is not yet decided, according to Quanjer (1936). Hoggan (1933) and Roland (1936) state that the same virus causes different types of symptoms in different leaves of the same plant. Verplancke (1933) described "speckled, veined, marbled, and pocked" types of mosaic.

In view of the various symptoms which develop with beet mosaic, Muraviov (1930) concluded it is possible that a virus complex is involved.

According to Smith (1934), "There is no evidence that more than one virus is concerned in the production of beet mosaic, and it is quite probable that the slightly different symptom expressions exhibited are due to the same agent."

After performing extensive inoculation experiments, Petherbridge and Stirrup (1935) concluded that the four types of symptoms which they studied are merely different aspects of one mosaic disease and are caused by a single virus.

It seems most unlikely that a yellows virus is involved in California or elsewhere in the United States. Sugar-beet-yellows virus has not been found in California or in any other sugar-beet district in this country. A disease called sugar-beet yellows (fusarium wilt) in the United States is caused by the soil fungus *Fusarium oxysporum* f. *betae* (Stewart) Syn. and Han.

Sugar-beet mosaic and curly top are sometimes found in the same plant in California, and some confusion in symptoms may result; the two viruses may be separated by the use of insect vectors (Severin, 1929). Another method of separating them is reported in a later section of this paper.

**Classification of the Virus.** Johnson and Hoggan (1935) in their key for plant viruses gave the chief diagnostic features of the sugar-beet-mosaic virus based on modes of transmission, properties of virus, and distinctive or specific symptoms.

Smith (1937) classifies the sugar-beet-mosaic virus as *Beta virus* 2 Lind, and lists the following synonyms: beet-yellows virus, Prillieux and Delacroix (1898); beet-mosaic virus, Lind (1915); sugar-beet virus 2, Johnson and Hoggan (1935); mosaic of sugar beet, Smith (1933).

Holmes (1939) classifies the sugar-beet-mosaic virus as *Marmor betae* in the family Marmoraceae and gives the following synonyms: beet-jaunisse virus, beet-yellows virus, beet-mosaic virus, sugar-beet virus 2, Beta virus 2.

McKinney (1944) established the "Genus 3. Poccile, gen. nov. as a synonym of *Marmor,* Holmes (1939) P.P."

Papers on properties of the virus are reviewed in connection with the work done on that aspect in the present investigation (page 497).

**Distribution of the Disease.** Prillieux and Delacroix (1898) observed the diseased beets in northern France in the vicinity of Paris in 1896. The distribution of beet mosaic, apart from the accidental presence of virus yellows in the same plants described by some investigators, on varieties of beets has been reported from Europe and Japan as follows:

Belgium: Verplancke (1933, 1934, 1934–35), De Haan and Roland (1935), Roland (1936)
Bohemia: Uzel, according to Molz (1926)
Denmark: Lind (1915)
England: Smith (1934, 1937), Petherbridge and Stirrup (1935), Ogilvie (1942), Moore (1943)
France: Lind (1915), Ducomet (1928, 1929)
Germany: Lind (1915), Molz (1926), Böning (1927*a*, *b*, *c*), Schmidt (1927, 1935)
Holland: Van der Meulen (1928), De Haan and Roland (1935), Quanjer (1936), Quanjer and Roland (1936), Roland (1936)
Russia: Proida (1930), Boryssewicz (1930), Muraviov (1930), Novinenko (1930), Shevtshenko (1930)
Sweden: Lind (1915), Eriksson (1912)
Japan: Hino (1933)

Conners (1935) was first to report mosaic on mangels in Canada as a disease new to that country. He also found a trace of a mosaic disease at Saskatoon on Swiss chard.

Townsend (1915) was the first to describe the symptoms of sugar-beet mosaic occurring in the middle and western portions of the United States. Reports from observers indicate that the disease on sugar beets, garden beets, and Swiss chard has become increasingly prevalent in this country. The distribution of sugar-beet mosaic as noted by those who have conducted specific investigations and by others who have conducted surveys of plant disease in various states in connection with the United States Bureau of Plant Industry is as follows:

California: Plant Disease Reporter[5] (1921*b*), Hoggan (1933), sent by C. W. Bennet
Colorado: Robbins (1921), Plant Disease Reporter (1921*b*, 1926, 1944)
Idaho: Hoggan (1933), sent by P. N. Annand
Indiana: Plant Disease Reporter (1921*a*,[6] 1923)
Kansas: Plant Disease Reporter (1921*b*, 1923)
Nebraska: Robbins (1921)
New Mexico: Plant Disease Reporter (1927, 1928*b*)
Texas: Plant Disease Reporter (1929)
Utah: Plant Disease Reporter (1928*a*, *b*, 1936)
Washington: Plant Disease Reporter (1930*a*, *b*, 1936), Jones (1931)
Wyoming: Plant Disease Reporter (1944)

**Economic Importance of the Disease.** Considerable differences have been reported in the economic importance of the disease in various countries.

[5] Numerous references of the occurrence of sugar-beet mosaic have appeared in the Plant Disease Reporter. They are listed in chronological order rather than under the names of the collaborators and editors in the "Appendix to Citations" at the end of the paper.

[6] In a personal interview, Gardner, the collaborator who sent in the report from Indiana in 1921, stated that the virus disease proved later to be sugar-beet savoy and not mosaic.

Prillieux and Delacroix (1898) stated that when plants are severely attacked, the roots do not increase much in size, but retain their normal sugar content; and that the total loss of the crop is about 50 per cent.

Molz (1926) estimated a reduction in yield of about 40 per cent in fields of mosaic sugar beets in Saale, Saxony.

Böning (1927*b*) estimated from field experiments at Bonn, Germany, that an average loss of 20 per cent resulted from mosaic, while the sugar content of fodder beets was reduced to one third of the normal. He also stated that development during the first year of the "curl mosaic," a severe form of the disease in which the leaves became curled and distorted, resulted the second year in stunted plants and poor seed production.

Shevtshenko (1930) calculated a reduction of 12.9 per cent in seed yield, and an average decrease in sugar content of 0.75 per cent in diseased sugar beets in the Kharkov district, U.S.S.R.

Prioda (1930) reported a maximum deficiency of sugar of 13 per cent as a result of the disease in the Kharkov district, U.S.S.R.

The economic importance of sugar-beet mosaic on beet seed plants has been discussed by five American plant pathologists. Robbins (1921) found scattered plants of sugar-beet seed plants in Colorado to be severely mottled, crumpled, twisted, and contorted, and the yield of seed reduced to a small amount. Crawford (Plant Disease Reporter, 1927; see Appendix to Citations) reported that mosaic caused considerable damage by dwarfing and stunting seed beets in New Mexico. Linford (Plant Disease Reporter, 1928*a*) mentioned that although mosaic had been known for several years in Utah, it had nowhere proved important. According to Jones (1931), growers and seedsmen contended that sugar-beet mosaic had reduced the yield of garden-beet seed at least 50 per cent on 1,200 to 1,500 acres in Skagit County, Washington, during the preceding five years. Conners (1935) estimated that about 5 per cent of the mangels grown for seed on Lulu Island near Vancouver were infected.

**Soil Transmission.** Robbins (1921) suggested the possibility that the virus might overwinter in the soil; but Böning (1927*a*) proved that the soil plays no part in transmission of the disease. Other writers who have discredited the possibility of soil transmission of the disease are Shevtshenko (1930), Jones (1931), and Verplancke (1933, 1934). Smith (1934) mentioned that most workers are agreed that the virus of beet mosaic is not carried in the soil.

**Seed Transmission.** With the exception of Ducomet (1929) and Verplancke (1933), investigators in general are not of the opinion that the virus is seed-borne. The latter reported that he had confirmed Ducomet's results by obtaining seed transmission in 7.1 per cent of the beets grown from seeds of mosaic mother-beets 2 months after growth aboveground. Petherbridge and Stirrup (1935) pointed out, however, that 2 months appears to be a somewhat lengthy period for the development of the symptoms; and the possibility of accidental infection by insects or other means naturally suggests itself.

Lind (1915), Böning (1927*b*), and Van der Meulen (1928) all concluded that the virus is not seed-transmitted.

To quote Quanjer (1936): "Contrary to what Verplancke (1933) claims to have found, the disease is not seed-transmissible. He claims to have cor-

roborated Ducomet's view in this respect, but this claim is based on a misunderstanding of what Ducomet (1929) wrote."

**Insect Transmission.** The following species of aphids have been recorded in the literature as vectors of the sugar-beet-mosaic virus:

Green peach aphid, *Myzus persicae* (Sulzer): Robbins (1921), Van der Meulen (1928), Jones (1931), Verplancke (1933), Hoggan (1933), Smith (1934), Petherbridge and Stirrup (1935), and Roland (1936)

Black beet or bean aphid, *Aphis fabae* Scopoli: Böning (1927*a*, 1927*b*, 1927*c*), Schaffnit (1927), Novinenko (1930), Verplancke (1933) [*Dorsalis fabae* (Scopoli) = *A. fabae*], Smith (1934), Petherbridge and Stirrup (1935), and Ogilvie (1942)

*Macrosiphum cognatus* Fieber: Novinenko (1930)

*Macrosiphum pelargonii* (Kaltenbach): Böning (1927*b*), Schaffnit and Weber (1927), and Verplancke (1933)

Potato aphid, *Macrosiphum solanifolii* (Ashmead) (= *M. gei* Kaltenbach and *M. ulmariae* Shrank): Van der Meulin (1928), Hoggan (1933). Smith (1934) failed to transmit the sugar-beet-mosaic virus with this species

Pound (1947) reported that the black bean aphid, *Aphis fabae,* and the green peach aphid, *Myzus persicae,* found commonly in beet fields in the Puget Sound section, are vectors of the virus. He obtained transmission of the virus with the cabbage aphid, *Brevicoryne brassicae,* but did not think that this insect is a common vector.

**Overwintering of Virus.** Prillieux and Delacroix (1898) noticed that diseased beets planted for seed in the spring developed symptoms on the new leaves.

Robbins (1921) demonstrated that the virus retained its vitality in the steckling throughout the silo period and stated that this was the only means of overwintering then known.

Böning (1927*a*) suggested the virus overwinters in frost-resistant spinach and seed beets.

Jones (1931) reported that the disease will overwinter in the beet roots in the pits, and such infected mother-beets act as a source of infection when planted in the field the following spring.

Quanjer (1936) stated that the virus remains in the roots destined for seed production.

**Host Range.** A number of investigators have briefly reported sugar-beet mosaic on some hosts among economic plants.

Lind (1915) reported mosaic on garden beets in Denmark, Sweden, France, and Germany, but stated that the disease was never found on sugar beets.

According to Böning (1927*a*) mosaic disease of beets is widespread in Germany on all cultivated varieties of beets. In another paper Böning (1927*b*) reported aphid transmission of the virus from beets to spinach and vice versa. Spinach was injured much more severely than beets. He also succeeded in transferring the virus from spinach to mangels and vice versa, and suggested that the two mosaics are closely related, if not identical (Böning, 1927*c*).

Van der Meulen (1928) failed in all attempts on intertransmission of the virus from beets to spinach by means of aphids.

Hoggan (1933) infected Bloomsdale and Virginia Savoy spinach with the virus by mechanical inoculation and produced local symptoms on Havana-type tobacco (*Nicotiana tabacum*) by infective aphids.

Smith (1934) transmitted the virus by mechanical inoculation or aphids to sugar beets, mangels, garden beets, spinach beets, sea-kale beets (chard), and spinach, and stated that no varieties of sugar beets or mangels resistant to mosaic are known.

Petherbridge and Stirrup (1935) mentioned that infection of turnips, tobacco, spinach, and beans with the virus of sugar-beet mosaic has been proved, but no evidence was given to substantiate their statement.

De Haan and Roland (1935) stated that in Holland mosaic is found more frequently on fodder beets than on sugar beets.

Pound (1947) reported that the sugar-beet mosaic virus infects all chenopodiaceous plants by mechanical inoculation. Of the species tested in seven other families, the virus infected only *Verbena hybrida, Viola tricolor, Stellaria media, Tetragonia expansa, Aster amellus, Zinnia elegans, Amaranthus retroflexus, Capsella bursa-pastoris,* and *Iodanthus pinnatifidus.* The first two of these host plants were symptomless carriers.

Six weeds in the family Chenopodiaceae have been experimentally infected with mosaic (Severin and Drake, 1947).

## MATERIALS AND METHODS

**Source of Virus.** The original sugar-beet-mosaic virus was obtained from a field of naturally infected sugar beets near San Pablo, California. Mechanical inoculation of healthy sugar beets grown under cover in the greenhouse was carried out to obtain a virus supply, and this was maintained by continuous inoculations during the experiments.

**Virus Extract.** In the preparation of the virus extract used in mechanical inoculations, the blades and petioles from infected plants were washed in distilled water and reduced to a pulp in a sterile mortar or food chopper. Juice was pressed from the pulp through two layers of cheesecloth into sterile containers. Methods used in determining properties of the virus are given in the section on that subject.

**Mechanical Inoculation.** Mechanical inoculations were performed essentially by the same method as described by Rawlins and Tompkins (1936). Cotton swabs on wooden splints were used; these were discarded and the hands were carefully washed after each trial or series of inoculations. The plants were washed with water shortly after inoculation to remove the inoculum and carborundum, and to prevent wilting.

**Production of Noninfective Aphids.** The green peach aphid, *Myzus persicae* (Sulzer), was used in most tests. Noninfective aphids were obtained by transferring mature, apterous aphids from populations collected in the field to favorable healthy host plants. On the following day the offspring from the mature aphids were transferred to a second healthy plant and allowed to multiply. Populations of noninfective aphids were maintained on healthy plants. No symptoms appeared on these plants. To test whether the populations remained noninfective, frequent checks were made on plants on which the noninfective aphids were reared, by removing a leaf and inoculating the extracted juice into healthy beets. The disease was not produced in any case.

Various sizes of lawn-covered insect cages with glass fronts and circular wooden bases, as described in a previous paper (Severin, 1930), were used in

confining aphid populations or lots of aphids transferred to beets during the experiments. The beets were exposed to aphids for at least 2 days, then were fumigated with Nicofume tobacco-paper insecticide, and placed in insect-proof cages for symptoms to develop.

**Methods of Transferring Aphids.** Transfers of noninfective or infective aphids to healthy host plants or to diseased beets were made by cutting off leaves carrying high populations and placing them on the inner leaves, whenever a new food supply was necessary. In those experiments requiring accurate counts of the number of aphids used, the insects were transferred from plant to plant with a moistened camel's-hair brush. Precautions were taken not to injure them in any way.

**Segregation of Plants.** Inoculated host plants were held for observation of symptoms in an insect-proof cage. Any plants on which symptoms developed were removed to another cage. If no symptoms appeared at the end of one month, the plants were discarded. Healthy plants were kept in a separate insect-proof cage.

## HOST RANGE, INCUBATION PERIOD OF DISEASE, AND RECOVERY OF VIRUS

**Economic Plants Naturally Infected.** The following economic plants in two families were demonstrated to be naturally infected with sugar-beet mosaic in California. The virus was recovered from these host plants and transferred to sugar beets by mechanical inoculation.

Chenopodiaceae:

*Beta maritima*
*Beta vulgaris*, sugar beet, mangel or stock beet, and garden, table, or red beet
*Beta vulgaris* var. *cicla*, Swiss chard
*Spinacia oleracea*, spinach

Aizoaceae:

*Tetragonia expansa*, New Zealand spinach

**Economic Plants Experimentally Infected.** The number of species and varieties of host plants experimentally infected with sugar-beet mosaic, the incubation period of the disease, and the recovery of the virus are shown in table 1.

**Nonsusceptible Economic Plants.** The following economic plants, tested by mechanical inoculation, were nonsusceptible to sugar-beet mosaic. An attempt was made to recover the virus from all plants which failed to show symptoms.

Cruciferae:

*Brassica oleraceae* var. *botrytis*, cauliflower (February variety)
*Brassica oleraceae* var. *capitata*, cabbage (Winter Colma variety)
*Mathiola incana* var. *annua*, annual stock or gilliflower

Cucurbitaceae:

*Cucumis sativus*, cucumber (White Spine variety)

Leguminosae:

*Phaseolus vulgaris*, bean (Lady Washington variety)
*Vicia faba*, horse bean

TABLE 1

HOST RANGE OF SUGAR-BEET MOSAIC, INCUBATION PERIOD OF DISEASE, AND RECOVERY OF VIRUS

| Common and scientific name of plant, and variety | Number of plants inoculated | Plants infected | Incubation period of disease, days | | Recovery of virus | |
|---|---|---|---|---|---|---|
| | | | Range | Average | Sugar beets inoculated | Sugar beets infected |
| **Chenopodiaceae, goosefoot or saltbush family** | | | | | | |
| *Beta maritima* | 10 | 10 | 9–15 | 10.3 | 10 | 10 |
| Sugar beet (*Beta vulgaris*) | | | | | | |
| Klein Wanzleben | 5 | 5 | 6–7 | 6.8 | 5 | 5 |
| A. 600 | 20 | 19 | 8–11 | 9.2 | .. | .. |
| U.S. No. 12 | 20 | 20 | 8–11 | 9.0 | .. | .. |
| U.S. No. 14 | 20 | 20 | 8–11 | 8.4 | .. | .. |
| U.S. No. 33 | 20 | 19 | 8–13 | 12.6 | .. | .. |
| U.S. No. 35 | 20 | 18 | 8–13 | 10.6 | .. | .. |
| Mangel or stock beet (*Beta vulgaris*) | | | | | | |
| Danish Sludstrup | 5 | 5 | 7–9 | 8.2 | 5 | 5 |
| Rose Top Giant Half Sugar | 5 | 5 | 7–9 | 8.0 | 5 | 5 |
| Golden Tankard | 10 | 10 | 7–8 | 7.3 | 10 | 10 |
| Red Eckendorf | 5 | 5 | 6–9 | 7.4 | 5 | 5 |
| Yellow Eckendorf | 5 | 5 | 7–8 | 7.6 | 5 | 4 |
| Garden beet (*Beta vulgaris*) | | | | | | |
| Crimson King | 5 | 5 | 6–7 | 6.2 | 5 | 4 |
| Crosby's Egyptian | 5 | 5 | 6 | 6.0 | 5 | 5 |
| Dark Red Ferry's strain | 5 | 5 | 6 | 6.4 | 5 | 3 |
| Dark Red Morse's strain | 5 | 5 | 6–7 | 6.4 | 5 | 5 |
| Extra Early Flat Egyptian | 5 | 5 | 6–8 | 6.6 | 5 | 5 |
| Good for All | 5 | 5 | 6–7 | 6.4 | 5 | 5 |
| New Century | 5 | 5 | 6–8 | 7.0 | 5 | 5 |
| Swiss chard (*Beta vulgaris* var. *cicla*) | | | | | | |
| Large-ribbed Dark Green | 10 | 9 | 6–14 | 11.5 | 10 | 10 |
| Large-ribbed White | 20 | 17 | 7–19 | 11.6 | 20 | 20 |
| Lucullus | 10 | 10 | 6–9 | 7.5 | 5 | 5 |
| Spinach (*Spinacia oleraceae*) | | | | | | |
| Giant Thick-leafed Nobel | 10 | 9 | 8–11 | 9.2 | 10 | 9 |
| Long Standing Bloomsdale | 15 | 14 | 8–15 | 10.6 | 15 | 14 |
| Prickly Seeded | 10 | 10 | 7–11 | 9.3 | 10 | 10 |
| Virginia Savoy | 5 | 5 | 11–15 | 13.2 | 10 | 9 |
| Viroflay | 10 | 10 | 7–12 | 8.3 | 10 | 9 |
| Common summer-cypress (*Kochia scoparia* var. *trichophila*) | 10 | 7 | 7–9 | .... | 10 | 5 |
| **Aizoaceae, carpet-weed family** | | | | | | |
| New Zealand spinach (*Tetragonia expansa*) | 10 | 7 | 8–12 | 10.6 | 10 | 9 |
| **Solanaceae, nightshade family** | | | | | | |
| Tobacco (*Nicotiana tabacum*) | | | | | | |
| Havana-type (local lesions) | .. | .. | .... | .... | .. | .. |
| Primus (local lesions) | .. | .. | .... | .... | .. | .. |

Solanaceae:
*Capsicum frutescens* var. *grossum*, bell pepper (California Wonder variety)
*Lycopersicon esculentum*, tomato (Marglobe and Santa Clara Canner varieties)
*Nicotiana glutinosa*
Umbelliferae:
*Apium graveolens* var. *dulce*, celery (Golden Self-blanching variety)

## SYMPTOMATOLOGY

**Beta maritima.** The sugar beet is presumably a derivative of *Beta maritima* indigenous to the Mediterranean region of Europe.

The early symptoms on *Beta maritima* are cleared veins and veinlets on the lower leaves of the apical and axillary shoots occurring simultaneously with, or closely following, stunting of the growing tips (plate 1, *A*). A chlorotic mottling follows rapidly after the clearing of the veinlets. The young leaves are curled downward, frequently cupped inward or outward, the margins rolled inward and often twisted (plate 1,*A*).

Small necrotic rings and larger necrotic areas appear on the older growing leaves, usually within 13 days after inoculation. The necrotic areas are located interveinally and some extend along the midrib or lateral veins. Sometimes a reddish discoloration of the midrib or lateral veins occurs, which later develops into necrotic areas. Necrosis of a portion or all of the leaf margins occurs and sometimes extends along the petiole to its attachment. Converging of advancing necrotic margins from opposite sides results in death of the leaf, while necrosis advancing between the lateral veins toward the midrib results in killing of the tissues on one side. Mature leaves did not become perceptibly chlorotic or necrotic. Dark streaks appear on the stem and later become sunken and necrotic (plate 1, *A*).

The sepals turn black and necrosis spreads to other flower parts, resulting in death of the flowers. The plants usually died within 3 or 4 weeks after inoculation.

The incubation period of the disease in the greenhouse was 9 to 15 days (table 1).

**Sugar Beet.** The symptoms on sugar beets are so diverse that, as noted earlier, some plant pathologists have suggested that more than one virus may be concerned in the production of the disease. It was considered advisable to present a detailed description of the sequence of symptoms observed on the leaves of sugar beets.

The first evidence of infection in nearly all cases, and one not readily discernible upon cursory observation, was the presence of a few, minute yellow or pale-green flecks (plate 2, *A*) on the youngest leaves, as if the juncture of two veinlets had become cleared and slightly widened (plate 2, *B*). This condition becomes apparent only when the leaves are held toward the light. A few hours later a definite clearing of the veinlets occurs (plate 4, *A*), usually spreading within 24 hours over the entire leaf (plate 4, *B*).

On a few occasions the first symptom to appear on the youngest leaves is small, scattered, chlorotic dots and irregular, chlorotic areas (plate 2, *D*), which gradually enlarge (plate 2, *E*) into a mottled pattern in later stages. In our observations, this was the exception, rather than the rule, contrary to the observations of Smith (1934).

Widening and merging of chlorotic areas along the cleared veinlets (plate 4, *C*) marks the beginning of an irregular blotching type of chlorosis. During or at the inception of this condition, the leaves in adjacent whorls begin to take on either a diffuse or a well-defined blotching type of chlorotic mottling. The mosaic pattern may consist of green blotches in a faintly chlorotic leaf (plate 3, *A*) or well-defined chlorotic blotches in the green portion of the leaf (plate 3, *C*). Young and older leaves rapidly become chlorotic (plates 2, *I*; 3, *B*), to such an extent that a few green areas appear in sharp contrast on a chlorotic background (plate 3, *D, F*). Young leaves often become crinkled along the margin; and sometimes large, deep-green, blisterlike elevations develop on the upper surface (plate 3, *E*), while other leaves from the same plant may not show the blisterlike elevations (plate 3, *G*).

Later, 3 weeks after inoculation, the blotching type of chlorosis was frequently replaced, particularly on the intermediate leaves, with a different pattern. This consisted for the most part of various sizes of chlorotic rings with normal green centers (plate 6, *A*); or numerous, scattered, chlorotic dots (plate 2, *C*) on the intermediate leaves of the same plant, or a mixture of both.

Unusual types of symptoms were observed occasionally on young leaves after clearing of the veinlets. In one of these, chlorosis was restricted to interveinal spaces (plate 2, *F*) and a veinbanding of normal green tissue occurs. Some leaves show but a few scattered dots or small, chlorotic areas which enlarge very slowly, if at all (plate 2, *D*). In another type a chlorotic band extends the length of the midrib and partly along some of the lateral veins (plate 2, *G*).

Under natural conditions, sugar beets in an advanced stage of the disease often show a necrosis of the midrib, veins, and petioles; and this sometimes occurs on experimentally infected plants (plate 2, *H*).

A dwarfing of the heart leaves of infected beet seedlings usually occurs; however, there was a general tendency to grow out of the stunting, and even at times to outgrow the symptoms, as previously noted by Robbins (1921).

Temperature influences the incubation period and the severity of symptoms. Under greenhouse conditions the period between inoculation and appearance of cleared veinlets ranged between 6 and 13 days (table 1). On October 26, 1936, 10 beet seedlings were inoculated with juice from one mosaic beet. Five of these were kept in the greenhouse, and the remaining 5 were placed in screened cages outdoors. The average time required for symptoms to develop on the beets in the greenhouse was 7.8 days. Mottling appeared on all the leaves within a week after symptoms first appeared. The 5 plants kept outdoors required an average of 25.2 days for symptoms to develop, and chlorosis was confined to the inner whorl of leaves. Two weeks after symptoms appeared, these plants were brought in the greenhouse, and symptoms appeared on the outer leaves within 5 days.

**Mangels, or Stock Beets.** The foliage symptoms of sugar-beet mosaic on varieties of mangels, or stock beets, were essentially the same as those on sugar beets; hence they will not be described.

Attempts to infect five varieties of mangels by mechanical inoculation were successful in 100 per cent of the trials (table 1). The incubation period of the disease in the greenhouse was 6 to 9 days (table 1).

**Garden, Table, or Red Beets.** Seven varieties of garden, table, or red beets were inoculated with the sugar-beet-mosaic virus, and no marked difference in the symptoms was noticed; hence those observed on Crosby's Egyptian beets will be described as typical for all varieties.

In the early phases of symptom production, cleared veinlets (plate 5, *A*) developed in the same manner as that described on the young leaves of sugar-beet seedlings. Stunting, crinkling, small blisterlike elevations, and malformations on the youngest leaves (plate 5, *B*) sometimes occur, but as growth continued, normal-shaped leaves are produced and dwarfing is largely overcome. Interveinal chlorosis (plate 5, *H*) sometimes appears on the intermediate leaves, and a predominance of small, chlorotic dots and irregular areas (plate 5, *C*) margined with red were observed on the outer leaves.

The most striking symptom is rings margined with red, which begin to develop on the older leaves 10 days after inoculation. Small red rings each surrounding a chlorotic center (plate 5, *D*) may appear, which frequently fuse (plate 5, *E*). More often, however, large red rings, varying from less than 1 mm to 4 mm in diameter, occur on the outer leaves. Sometimes wide, outer red rings appear, each with an inner, chlorotic ring enclosing a pale-red center (plate 5, *F*). The rings frequently coalesce (plate 5, *G*). In a later stage of the disease, a necrotic center appears, which enlarges in the ring, and may drop out and leave a hole in the leaf.

The incubation period of the disease in the greenhouse varied from 6 days to 8 in the seven varieties of garden beets tested (table 1).

**Swiss Chard.** A departure from the cleared veinlets as the first symptom was noted in Large-ribbed White Swiss chard. The first symptom to appear on the youngest leaves is a few small, scattered, chlorotic dots (plate 7, *A*); these enlarge into chlorotic blotches involving most of the leaf surface. The older leaves usually show a predominance of chlorotic rings with green centers and finely striated borders (plate 6, *B*). Sometimes the chlorotic rings coalesce. Small chlorotic dots usually are intermingled with the rings.

A clearing of the veinlets (plate 7, *B*) was the first symptom to develop on Large-ribbed Dark Green and Lucullus varieties of Swiss chard, followed by interveinal chlorosis and mottling, and by chlorotic rings surrounding green centers (plate 6, *B*).

Naturally infected young Swiss chard obtained from San Pablo, September 30, 1936, showed chlorotic blotching and some rings, but was not noticeably stunted. Naturally infected old plants of Large-ribbed Swiss chard collected from Bay Farm Island on February 1, 1937, were severely stunted and malformed, with mottled leaves. After being potted and kept in the greenhouse, new leaves developed from the center and from adventitious shoots around the crown. Most of the young leaves were severely crinkled along the margins and malformed. Blisterlike elevations (plate 7, *C*), confined chiefly to the leaf margin, were common on the chlorotic leaves. Other leaves from the same plant were malformed (plate 7, *D*) but not mottled. The tips of the leaves may turn dark yellow or orange and necrosis occurs.

Three varieties of Swiss chard—Large-ribbed Dark Green, Large-ribbed White, and Lucullus—were inoculated with the juice from mosaic beets. The virus was recovered in 100 per cent of the trials, as shown in table 1. The incu-

bation period of the disease in the greenhouse varied from 6 to 19 days in the three varieties of Swiss chard infected with the sugar-beet-mosaic virus (table 1).

**Spinach.** Spinach was demonstrated to be naturally infected with beet mosaic in vegetable gardens near San Pablo. The virus extract from diseased spinach collected in the field was inoculated into healthy spinach and sugar-beet plants, and typical symptoms of beet mosaic developed (plate 1, *B*). The symptoms are described in another paper (Severin, 1948).

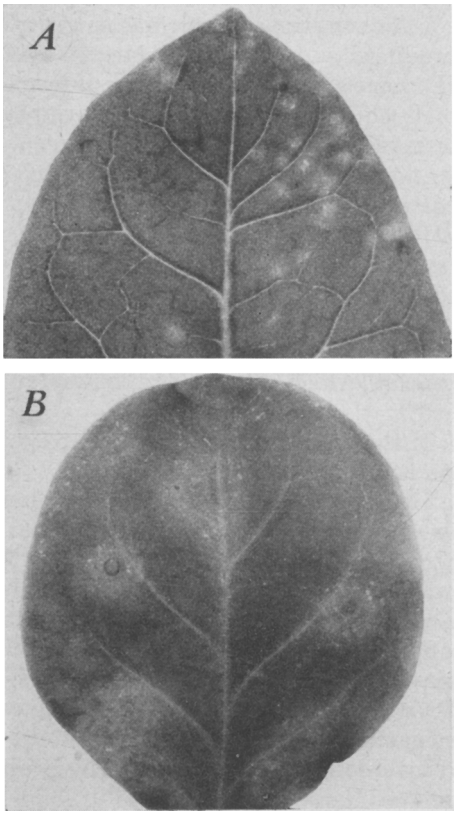


Fig. 1. Local symptoms of sugar-beet mosaic on the tobacco leaves on which the green peach aphid (*Myzus persicae*) had fed: *A*, Havana tobacco (*Nicotiana tabacum*) leaf showing chlorotic, circular areas, sometimes with a pinpoint necrotic center; *B*, Primus tobacco (*N. tabacum*) leaf showing concentric rings.

The incubation of the disease varied from 7 to 15 days in the five varieties of spinach experimentally infected with beet mosaic (table 1).

**Common Summer Cypress.** The foliage symptoms of sugar-beet mosaic on common summer cypress were not evident, but the apical shoots of the branches were stunted within 9 days after inoculation. A slight upward curling of the tips of the long, narrow leaves occurs. Seven of 10 plants inoculated showed symptoms. Inoculations of the extract from the 10 plants experimentally infected to healthy sugar beets resulted in recovery of the virus in 5 of the 10 sugar beets inoculated, as shown in table 1.

**New Zealand Spinach.** Systemic infection of New Zealand spinach resulted when healthy plants were inoculated with juice from mosaic sugar beets. The first symptoms on young leaves are small, irregular, chlorotic flecks along and between the veins. Older leaves develop chlorotic areas and veinbanding along the midrib and lateral veins (plate 8, *A*). On some of the larger leaves the surface is stippled with small, irregular, sunken dots (plate 8, *B*). In later stages of the disease, large, circular, chlorotic areas, 5 mm in diameter, occur on or between the veins of mature leaves. These rings become orange in color, each showing a darker, inner ring (plate 8, *C*), which later becomes necrotic. Sometimes necrosis of the circular areas spreads along the lateral veins to the leaf margin (plate 8, *D*). Growth of the apical and axillary shoots was retarded, but infected plants were still growing 8 weeks after inoculation.

**Havana-Type and Primus Tobaccos.** Hoggan (1933) failed to infect Havana-type tobacco by mechanical inoculation, but obtained local symptoms upon the leaves on which *Myzus persicae* and *Macrosiphum solanifolii* had fed; systemic infection did not follow. The virus was readily recovered from the tobacco leaves showing symptoms, by mechanically inoculating the extracted juice in the leaves of healthy sugar beets.

This work was repeated by feeding infective *Myzus persicae* on the leaves of a Havana-type variety and on Primus tobacco (*Nicotiana tabacum*). The leaves on which *M. persicae* was feeding showed circular, chlorotic areas, sometimes with a pinpoint, necrotic center (fig. 1, *A*), which is probably the feeding puncture. Leaves of Primus tobacco showed concentric rings (fig. 1, *B*). The virus extract from pieces of the leaves showing symptoms was inoculated into the leaves of healthy sugar-beet seedlings, and typical symptoms of sugar-beet mosaic developed.

## PROPERTIES OF THE VIRUS

The results of studies on the properties of the sugar-beet-mosaic virus conducted by Hoggan (1933) and Pound (1947) in the United States and by Verplancke (1934–35) in Belgium are compared below:

| | Hoggan | Verplancke | Pound |
|---|---|---|---|
| | + – | | |
| Longevity *in vitro* | 24–48 hours (70° F) | 6–7 days (20° C)<br>9–10 days (12° C) | 72 hours (20° C) |
| Tolerance to dilution | 1:1,000 | 1:100,000 | 1:2,000 |
| | + – | + – | |
| Thermal death point | 55°–60° C | 90°–95° C | 61° C (10 minutes) |

The differences between the results of Hoggan and those of Verplancke were explained by the latter on the grounds that there was probably more than one virus concerned in the production of sugar-beet mosaic.

Quanjer (1936) considered the property studies of Hoggan (1933) to be reliable but those of Verplancke (1934–35) to be valueless.

**Thermal Inactivation.** Undiluted, extracted juice from the blades and petioles of experimentally infected sugar beets was used in determining the thermal inactivation of the virus. Extractions were made 1 to 7, and 179 days after the first appearance of symptoms of the disease. Ten cc of diseased juice was poured into thin-walled Pyrex test tubes, over the mouths of which four thicknesses of fish swim-bladder membrane were tightly drawn and made watertight by means of rubber bands. The tubes were submerged upright in a water bath controlled by an electric thermostat. The water was kept in circulation to maintain a uniform temperature with a motor-driven agitator. A thermometer with 0.5° C gradations was suspended in the water at the depth at which the tubes were held. Determinations were made at 5°C intervals. The time of exposure in the water bath was 11 minutes, allowing 1 minute for heat to penetrate the glass. After exposure to the desired temperature, the tubes were quickly cooled in running water and the extracts were then used for inoculation. Unheated controls were used in all tests. The number of infections obtained by mechanical inoculation into 5 healthy sugar-beet seedlings in each trial is shown in table 2.

As shown in table 2, the virus remained active after heating 10 minutes at 50° and 55°C but was inactivated after heating to 60°. No apparent difference was exhibited between trials when extractions were made 1 to 7, or 179 days from the time symptoms first appeared. The results agree with those reported by Hoggan (1933).

**Effects of Freezing Virus Extract.** Virus extracts were obtained from mosaic-infected sugar beets, 98 to 100 days after symptoms first appeared. Ten cc of expressed juice was placed in cotton-plugged test tubes and kept in

TABLE 2

THERMAL INACTIVATION OF SUGAR-BEET-MOSAIC VIRUS*

| Temperature, ° C | Beets inoculated | Beets infected | Per cent infected |
|---|---|---|---|
| Unheated control | 25 | 23 | 92 |
| 50 | 25 | 17 | 68 |
| 55 | 25 | 7 | 28 |
| 60 | 25 | 0 | 0 |
| 65 | 25 | 0 | 0 |

* Combined results with extracts obtained 1 to 7 and 179 days after symptoms appeared.

TABLE 3

EFFECT OF FREEZING VIRUS EXTRACT OF SUGAR-BEET-MOSAIC KEPT IN COLD STORAGE AT –18° C

| Age of virus extract, months | Number of beets | | Per cent infected |
|---|---|---|---|
| | Inoculated | Infected | |
| Control | 25 | 25 | 100 |
| 1 | 25 | 23 | 92 |
| 2 | 25 | 5 | 20 |
| 3 | 25 | 2 | 8 |
| 4 | 25 | 1 | 4 |
| 5 | 25 | 0 | 0 |

a darkened, cold-storage room at –18°C. Inoculations of diseased juice were made at the time of extraction to serve as controls for each trial. The results obtained are stated in table 3.

As shown in table 3, all control plants became infected, and a marked decrease in the number of infections occurred after exposure for 2 months to a freezing temperature. A single infection out of 25 beets inoculated was obtained after 4 months, and no infections occurred after 5 months in cold storage at –18°C.

**Tolerance to Dilution.** The tolerance to dilution of the virus was determined with the juice expressed from blades and petioles of experimentally infected sugar beets at intervals varying from 1 to 3 days to 118 days from the time that symptoms first appeared. The diluent consisted of sterile distilled water. Different pipettes were used with each dilution. An undiluted control was used in each trial. The results with extracts prepared 1 to 3 days after symptoms appeared are given in table 4.


Plate 1. Symptoms of sugar-beet mosaic: *A*, on *Beta maritima*, showing stunting of apical and axillary shoots, chlorotic dots on older leaves, necrosis and drying of youngest leaves, blackening of sepals and other flower parts, and necrotic streaks on stem; *B*, on Long Standing Bloomsdale spinach (*Spinacia oleracea*), showing small chlorotic areas and cleared veinlets.

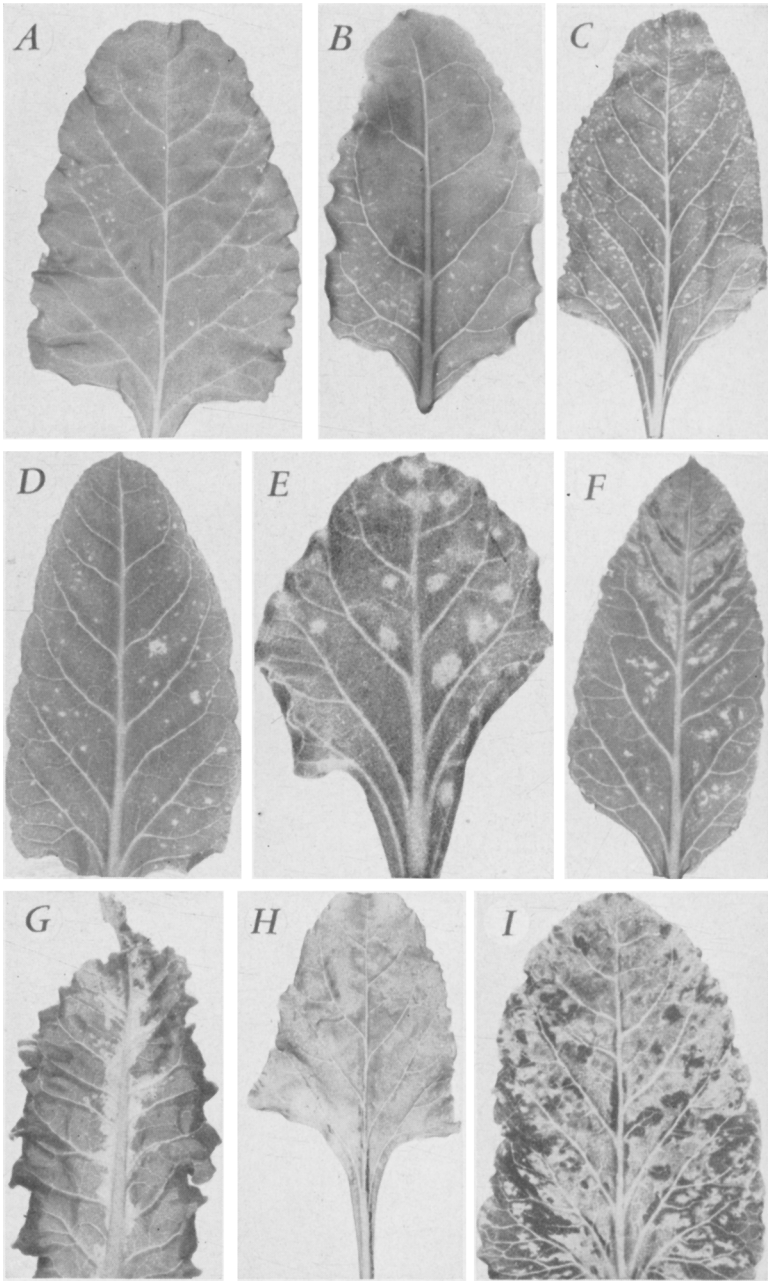


Plate 2. Sugar beet (*Beta vulgaris*) leaves showing symptoms of mosaic: *A*, minute yellow or pale-green flecks on youngest leaf, the first symptom of the disease; *B*, flecks and the veinlets beginning to clear; *C*, intermediate leaf, 3 weeks after inoculation, showing only chlorotic dots, taken from the same plant as the one that showed the ring pattern (plate 6, *A*). *D*, chlorotic dots and small, irregular, chlorotic areas; *E*, enlargements of chlorotic dots; *F*, interveinal chlorosis; *G*, chlorotic band extending along midrib and bases of lateral veins; *H*, necrosis of petiole and midrib. *I*, chlorosis of leaf, with chlorotic blotches.

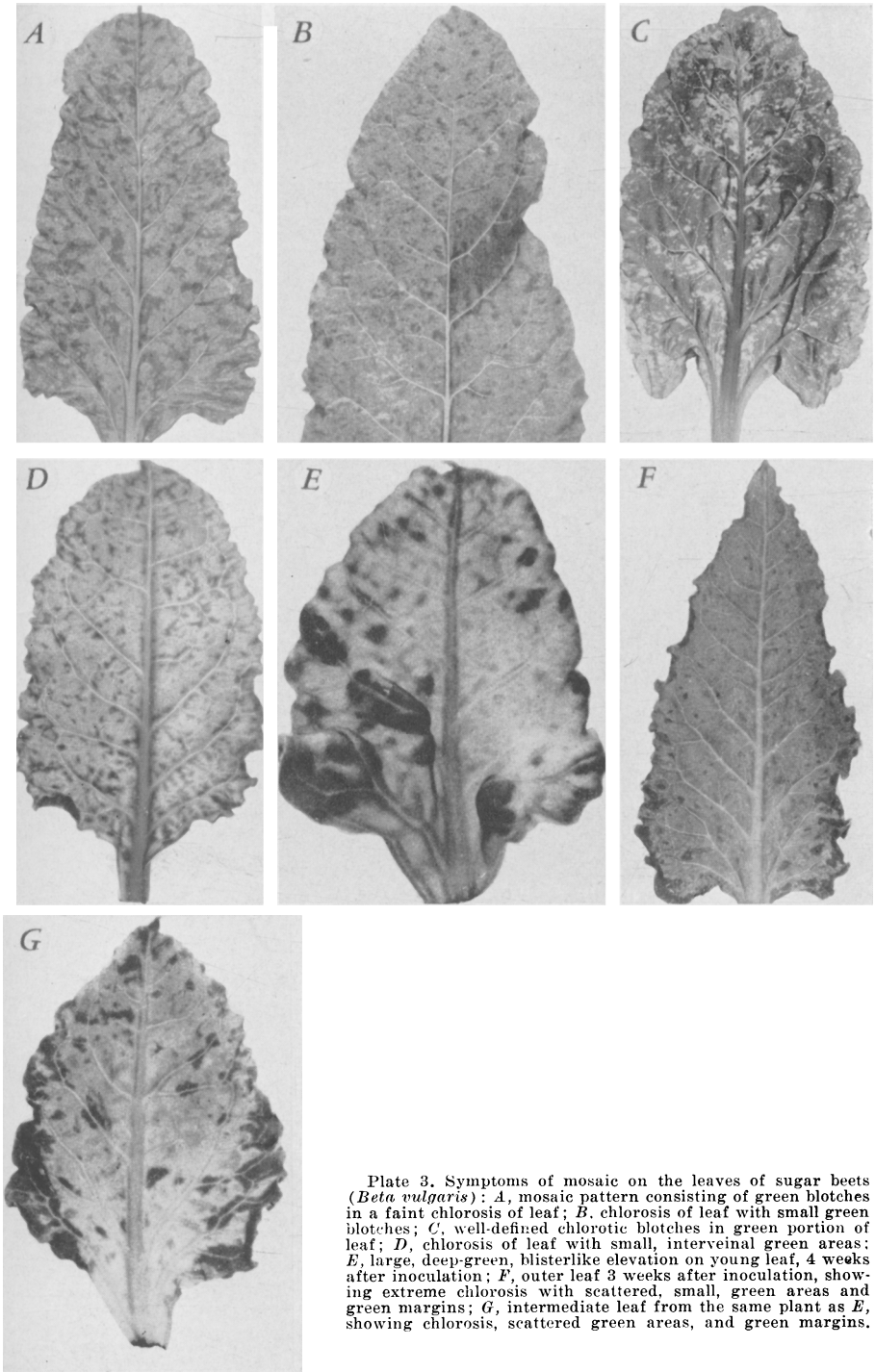


Plate 3. Symptoms of mosaic on the leaves of sugar beets (*Beta vulgaris*): *A*, mosaic pattern consisting of green blotches in a faint chlorosis of leaf; *B*, chlorosis of leaf with small green blotches; *C*, well-defined chlorotic blotches in green portion of leaf; *D*, chlorosis of leaf with small, interveinal green areas; *E*, large, deep-green, blisterlike elevation on young leaf, 4 weeks after inoculation; *F*, outer leaf 3 weeks after inoculation, showing extreme chlorosis with scattered, small, green areas and green margins; *G*, intermediate leaf from the same plant as *E*, showing chlorosis, scattered green areas, and green margins.

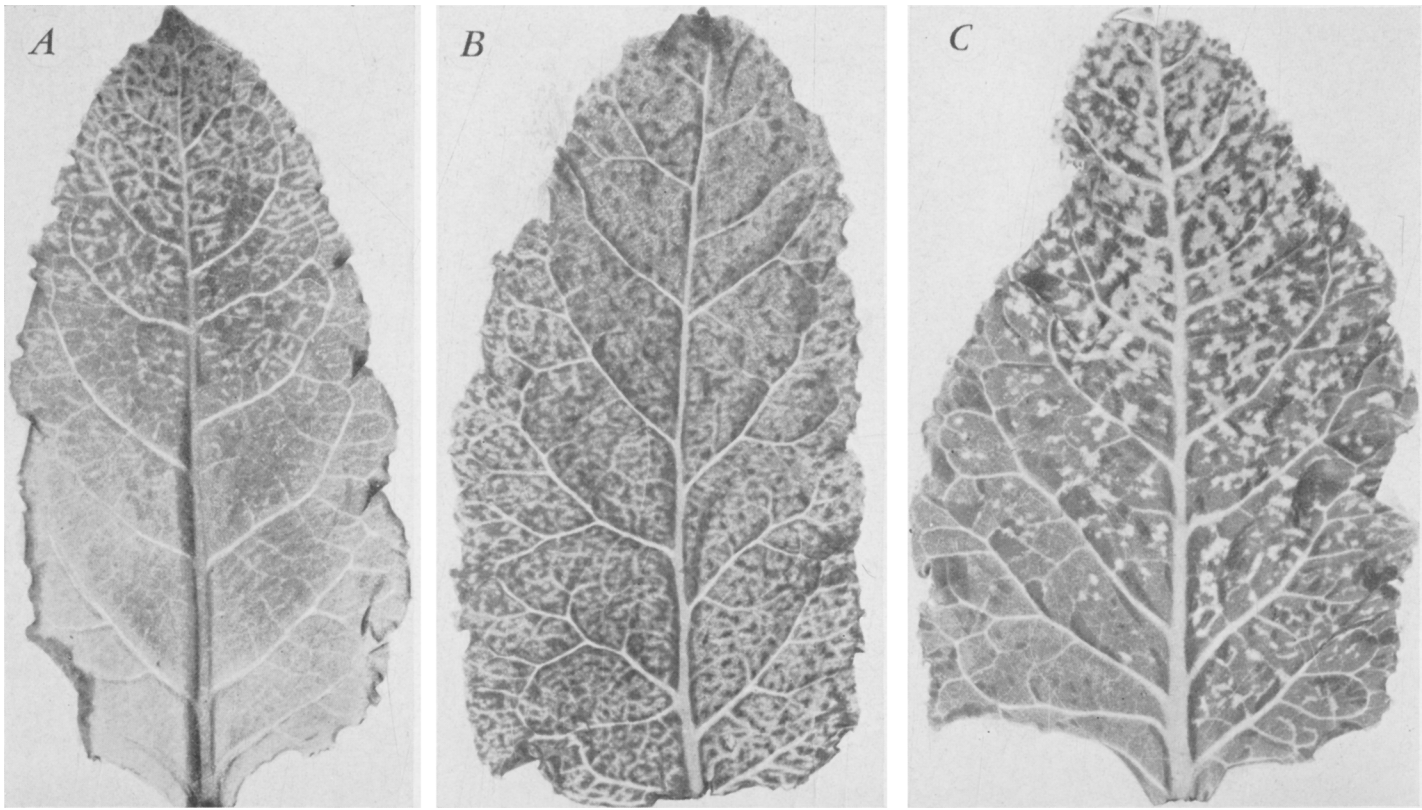


Plate 4. Sugar beet (*Beta vulgaris*) leaves showing symptoms of mosaic: *A*, network of cleared veinlets on upper half of leaf; *B*, cleared venation over entire leaf; *C*, widening and merging of chlorotic areas along cleared veinlets.

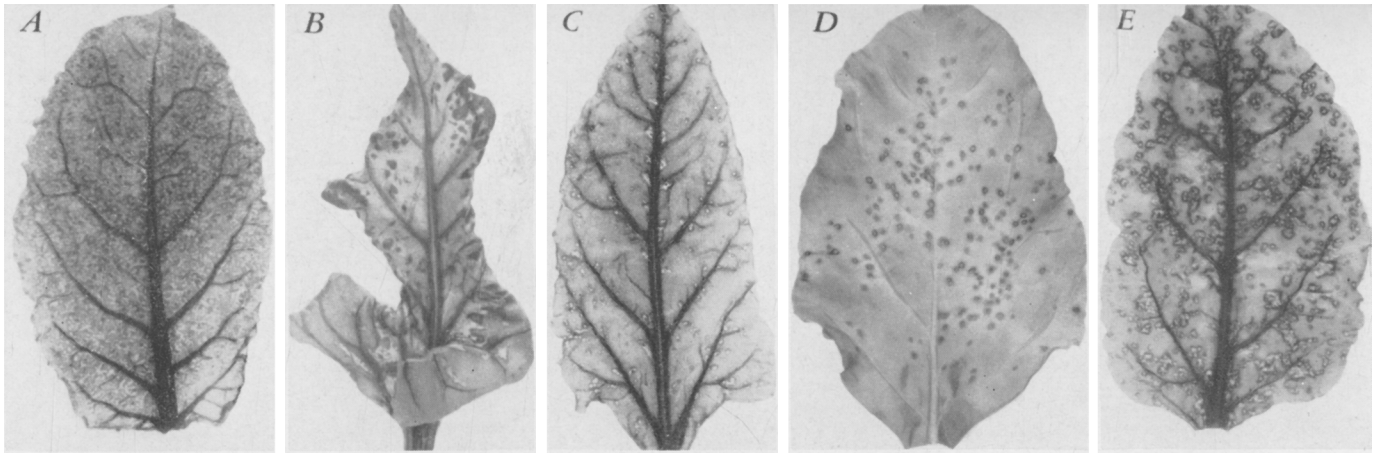


Plate 5. Symptoms of sugar-beet mosaic on leaves of Crosby's Egyptian red beets (*Beta vulgaris*): *A*, cleared veinlets on youngest leaf; *B*, malformation and small, blisterlike elevation in chlorotic areas of youngest leaf; *C*, small, chlorotic dots and irregular areas margined with red on outer leaf; *D*, small, red rings, each surrounding a chlorotic area; *E*, fusion of small, red rings; *F*, wide, outer red ring and inner, chlorotic ring enclosing a pale-red center; *G*, fusion of red rings; *H*, interveinal chlorosis on intermediate leaf.

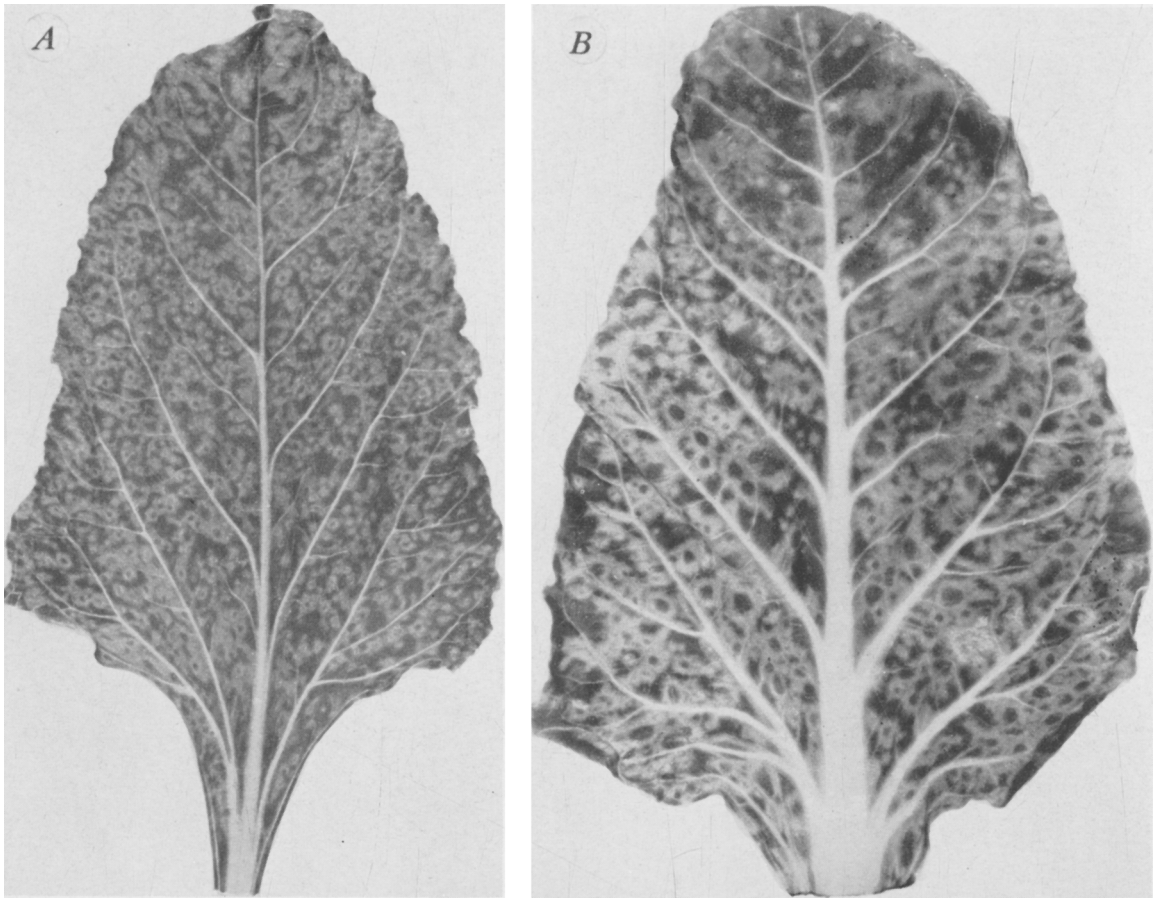


Plate 6. Symptoms of sugar-beet mosaic: *A*, on sugar beet (*Beta vulgaris*), showing chlorotic rings with green centers and numerous, scattered, chlorotic dots on intermediate leaf, 3 weeks after inoculation; *B*, on older leaf of Large-ribbed White Swiss chard (*Beta vulgaris* var. *cicla*), showing predominance of chlorotic rings with green centers and finely striated borders, some rings coalescing, and small chlorotic dots intermingled with the rings.

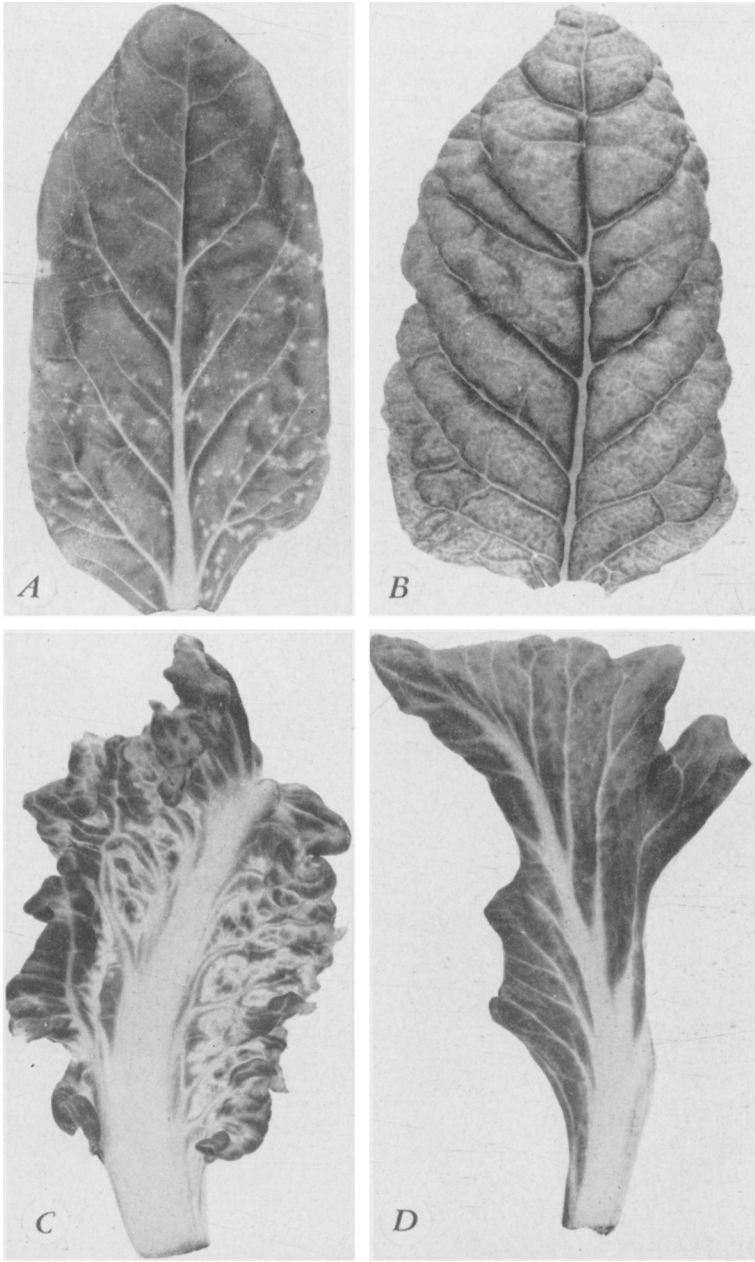


Plate 7. Varieties of Swiss chard (*Beta vulgaris* var. *cicla*) showing symptoms of sugar-beet mosaic: *A*, young leaf from the Large-ribbed White variety experimentally infected, showing scattered, small, chlorotic dots, the first symptom on this variety, 12 days after inoculation; *B*, young leaf from the Lucullus variety experimentally infected, showing cleared veinlets on entire leaf, the first symptom on this variety; *C*, young leaf from adventitious shoot of the Large-ribbed White variety naturally infected, showing malformation, crinkling of the margins, chlorosis, and blisterlike elevations; *E*, malformed leaf from another shoot showing no mosaic symptom.

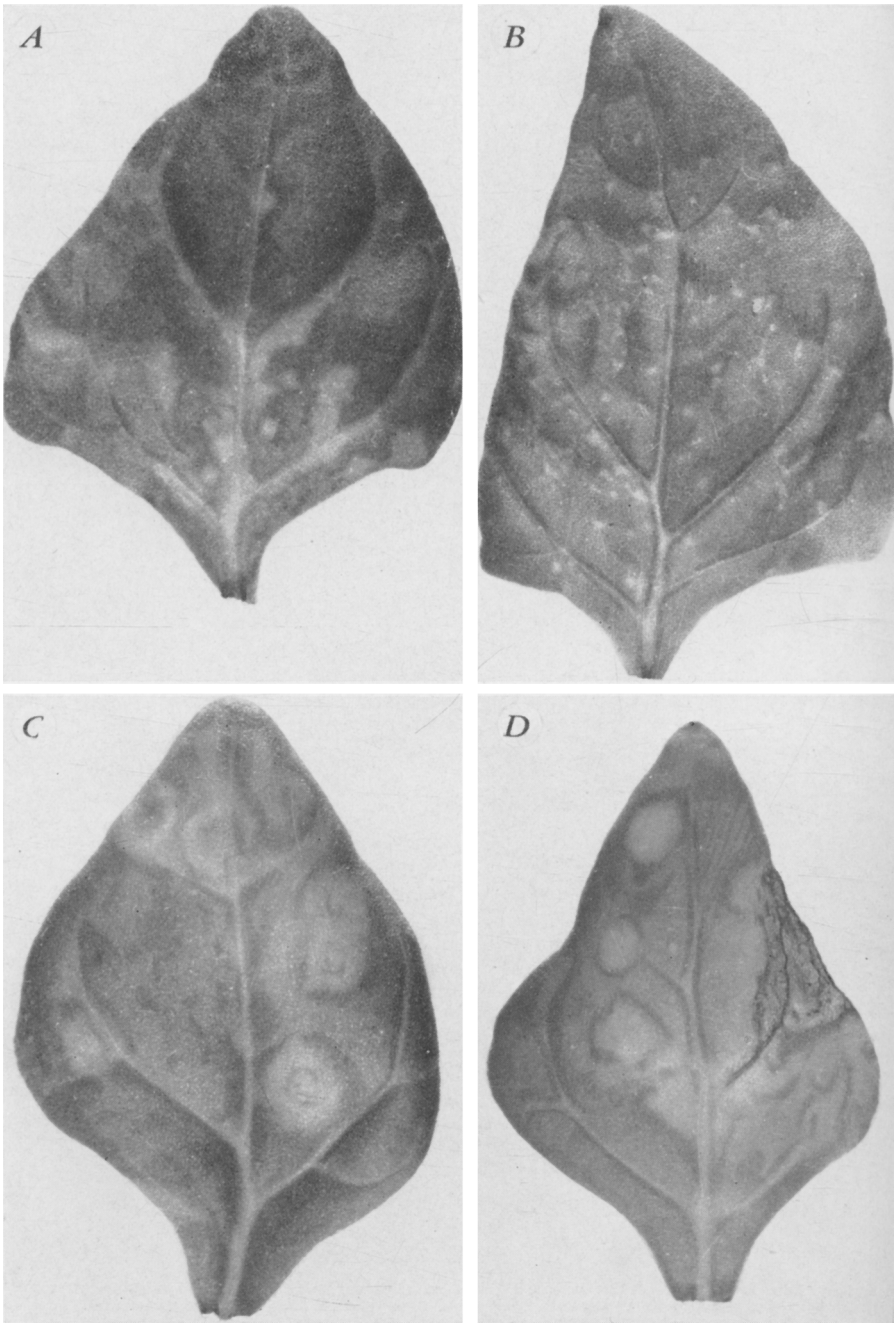


Plate 8.—Leaves of New Zealand spinach (*Tetragonia expansa*) showing symptoms of sugar-beet mosaic: *A*, older leaf showing chlorotic areas and veinbanding along the midrib and veins; *B*, outer leaf showing stippling with small, irregular, sunken dots; *C*, mature leaf showing large, circular, orange-colored areas, each with a darkened, inner ring; *D*, necrosis of circular area spreading along a lateral vein to the margin of the outer leaf.

As table 4 shows, tolerance to dilution of the virus extract was 1 : 5,000 for the extract obtained 1 to 3 days after symptoms first appeared. Extract obtained from plants 118 days after symptoms first developed gave no infections at a dilution of 1 : 500; and none was obtained at a dilution of 1 : 1,000 of extract from plants 107 days after symptoms were first evident. The results indicate that the dilution tolerance of the virus extract varied inversely with the number of days between the first appearance of symptoms and the extraction of the juice, though the same strain of virus was maintained throughout.

TABLE 4

TOLERANCE OF SUGAR-BEET-MOSAIC VIRUS* TO DILUTION

| Dilution | Number of beets | | Per cent infected |
|---|---|---|---|
| | Inoculated | Infected | |
| Undiluted control | 145 | 125 | 86 |
| 1:10 | 30 | 22 | 73 |
| 1:100 | 65 | 33 | 51 |
| 1:500 | 40 | 36 | 90 |
| 1:1,000 | 95 | 36 | 38 |
| 1:2,000 | 65 | 14 | 22 |
| 1:3,000 | 65 | 5 | 8 |
| 1:4,000 | 65 | 4 | 6 |
| 1:5,000 | 120 | 4 | 3 |
| 1:6,000 | 25 | 0 | 0 |
| 1:7,000 | 25 | 0 | 0 |
| 1:8,000 | 25 | 0 | 0 |
| 1:9,000 | 25 | 0 | 0 |
| 1:10,000 | 145 | 1 | 1 |
| 1:15,000 | 85 | 1 | 1 |
| 1:20,000 | 85 | 1 | 1 |
| 1:25,000 | 50 | 0 | 0 |

* Extract obtained 1 to 3 days after symptoms first appeared

Differences between the results presented in table 4 and those of Hoggan (1933), who reported a dilution to tolerance of 1 : 1,000, may be due to the use of more recently infected beets in this experiment than were used in her studies.

In later experiments in which the virus extract was obtained from small sugar beets shortly after symptoms appeared, only 1 infection occurred at each of the following dilutions: 1 : 10,000, 1 : 15,000, and 1 : 20,000, and none at 1 : 25,000 (table 4). Since no infections were obtained with dilutions of 1 : 6,000, 1 : 7,000, 1 : 8,000, and 1 : 9,000, the results with greater dilutions must be considered as errors. The inoculated beets were placed in cages enclosed with small-mesh, brass screen wire, but these cages did not eliminate ants, which may have carried infective aphids.

**Tolerance to Aging in Vitro.** To determine the resistance of the virus to aging *in vitro,* test tubes containing 10 cc of expressed juice from the blades and petioles of experimentally infected sugar beets were plugged with cotton and kept in the dark at room temperature. Fresh virus extract was used as a control in each trial. Mechanical inoculations to healthy beet seedlings were made at intervals varying from 3 to 144 hours to determine the infectivity of the virus. The results are shown in table 5.

As appears in table 5, the virus was active after exposure for 96 hours *in vitro* at room temperature but lost its infectivity after aging 144 hours, or 6 days. No difference in results was found in virus extracts obtained from plants 1 to 7 days and 107 days after symptoms first appeared.

Hoggan (1933) reported that but 2 of 20 plants were infected after 24 hours' aging and that no infections were obtained after 48 hours.

## INSECTS WHICH FAILED TO TRANSMIT VIRUS

All attempts to transmit the virus with insects exclusive of Aphididae failed. The following insects were tried: Say stinkbug, *Chlorochroa sayi* Stål, tarnished plant bug, *Lygus pratensis oblineatus* (Say); harlequin cabbage bug, *Murgantia histrionica* (Hahn); a white fly, *Asterochiton vittatus* (Quaintance); citrophilus mealybug, *Pseudococcus gahani* Green; short-winged aster leafhopper, *Macrosteles divisus* (Uhler); western potato leafhopper, *Empoasca abrupta* DeLong; and a cercopid, *Cixius cultus* Ball.

TABLE 5

TOLERANCE OF SUGAR-BEET-MOSAIC VIRUS TO AGING IN VITRO

| Hours exposed | Number of beets | | Per cent infected |
|---|---|---|---|
| | Inoculated | Infected | |
| 0 (control) | 100 | 97 | 97 |
| 3 | 25 | 20 | 80 |
| 6 | 25 | 10 | 40 |
| 12 | 25 | 10 | 40 |
| 18 | 25 | 7 | 28 |
| 24 | 75 | 36 | 48 |
| 48 | 100 | 30 | 30 |
| 60 | 75 | 23 | 31 |
| 72 | 75 | 13 | 17 |
| 96 | 5 | 1 | 20 |
| 144 | 5 | 0 | 0 |

## APHID TRANSMISSION OF THE VIRUS

**Vectors Reared on Mosaic-Infected Sugar Beets.** A comparison was made of the transmission of the virus by three aphid species reared on experimentally infected beets and by mechanical inoculation. The species used in this test were erigeron root aphid, *Aphis middletonii* (Thomas); pea aphid, *Macrosiphum pisi* (Kaltenbach); and green peach aphid, *Myzus persicae* (Sulzer). Each species was colonized on 5 infected sugar beets. The aphids were transferred in lots of 20 from each infected beet to 5 healthy beets, making a total of 25 trials for each species. In order to compare aphid transmission with mechanical inoculation, the virus extract from the infected plants on which the aphids had been reared was inoculated into 5 healthy beets.

As table 6 shows, *Aphis middletonii, Macrosiphum pisi,* and *Myzus persicae* transmitted the virus in 20, 60, and 56 per cent of the trials respectively. The infections obtained by mechanical inoculation averaged 98 per cent in all cases.

In another experiment, bean or dock aphid, *Aphis rumicis* Linnaeus, was colonized on 15 mosaic beets. As in the preceding experiment, the aphids were transferred in lots of 20 from each infected beet to 5 healthy beets; there was thus a total of 75 tests. Not a single infection resulted. Then 100 bean aphids

TABLE 6

TRANSMISSION OF SUGAR-BEET-MOSAIC VIRUS BY APHIDS REARED ON INFECTED BEETS AND BY MECHANICAL INOCULATION

| Aphid species and lot* no. | Aphid transmission | | Mechanical inoculation† | |
|---|---|---|---|---|
| | Beets inoculated | Beets infected | Beets inoculated | Beets infected |
| *Aphis middletonii:* | | | | |
| Lot 1 | 5 | 3 | 5 | 5 |
| Lot 2 | 5 | 1 | 5 | 5 |
| Lot 3 | 5 | 1 | 5 | 5 |
| Lot 4 | 5 | 0 | 5 | 5 |
| Lot 5 | 5 | 0 | 5 | 4 |
| Total | 25 | 5 | 25 | 24 |
| *Percentage* | .. | *20* | .. | *96* |
| *Macrosiphum pisi:* | | | | |
| Lot 1 | 5 | 4 | 5 | 5 |
| Lot 2 | 5 | 4 | 5 | 5 |
| Lot 3 | 5 | 3 | 5 | 5 |
| Lot 4 | 5 | 2 | 5 | 5 |
| Lot 5 | 5 | 2 | 5 | 4 |
| Total | 25 | 15 | 25 | 24 |
| *Percentage* | .. | *60* | .. | *96* |
| *Myzus persicae.* | | | | |
| Lot 1 | 5 | 5 | 5 | 5 |
| Lot 2 | 5 | 4 | 5 | 5 |
| Lot 3 | 5 | 4 | 5 | 5 |
| Lot 4 | 5 | 3 | 5 | 5 |
| Lot 5 | 5 | 3 | 5 | 5 |
| Lot 6 | 5 | 3 | 5 | 5 |
| Lot 7 | 5 | 2 | 5 | 4 |
| Lot 8 | 5 | 2 | 5 | 4 |
| Lot 9 | 5 | 1 | 5 | 5 |
| Lot 10 | 5 | 1 | 5 | 5 |
| Total | 50 | 28 | 50 | 48 |
| *Percentage* | .. | *56* | .. | *96* |

* 20 aphids per lot.

† Virus extract for mechanical inoculation was taken from the same diseased beet on which the corresponding lot of aphids fed.

reared on mosaic beets were transferred singly to healthy beets. One infection was obtained. It is evident that the bean aphid rarely transmits the virus.

**Vectors Reared on Other Host Plants.** Eleven species of aphids which have not been found to multiply on beets under natural conditions were tested, and found to be capable of transmitting the virus. The transmission of the virus from experimentally infected to healthy beets by ten of these species,

TABLE 7

TRANSMISSION OF SUGAR-BEET-MOSAIC VIRUS TO BEETS BY APHIDS REARED ON OTHER HOSTS AND BY MECHANICAL INOCULATION

| Aphid species, plant it was reared on, and lot* no. | Aphid transmission: Period on diseased beet, days | Aphid transmission: Beets inoculated | Aphid transmission: Beets infected | Mechanical inoculation†: Beets inoculated | Mechanical inoculation†: Beets infected |
|---|---|---|---|---|---|
| *Aphis apigraveolens* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 5 | 5 | 5 |
| Lot 2 | 2 | 5 | 4 | 5 | 5 |
| Lot 3 | 2 | 5 | 4 | 5 | 5 |
| Lot 4 | 2 | 5 | 3 | 5 | 5 |
| Lot 5 | 2 | 5 | 3 | 5 | 5 |
| Total | .. | 25 | 19 | 25 | 25 |
| *Percentage* | .. | .. | *76* | .. | *100* |
| *Aphis apii* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 4 | 5 | 4 |
| Lot 2 | 2 | 5 | 4 | 5 | 5 |
| Lot 3 | 2 | 5 | 3 | 5 | 5 |
| Lot 4 | 2 | 5 | 3 | 5 | 5 |
| Lot 5 | 2 | 5 | 2 | 5 | 5 |
| Total | .. | 25 | 16 | 25 | 24 |
| *Percentage* | .. | .. | *64* | .. | *96* |
| *Aphis ferruginea-striata* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 2 | 5 | 5 |
| Lot 2 | 2 | 5 | 0 | 5 | 5 |
| Lot 3 | 2 | 5 | 0 | 5 | 5 |
| Lot 4 | 2 | 5 | 0 | 5 | 5 |
| Lot 5 | 2 | 5 | 0 | 5 | 5 |
| Total | .. | 25 | 2 | 25 | 25 |
| *Percentage* | .. | .. | *8* | .. | *100* |
| *Aphis gossypii* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 4 | 5 | 5 |
| Lot 2 | 2 | 5 | 4 | 5 | 5 |
| Lot 3 | 2 | 5 | 2 | 5 | 5 |
| Lot 4 | 2 | 5 | 2 | 5 | 5 |
| Lot 5 | 2 | 5 | 2 | 5 | 5 |
| Total | .. | 25 | 14 | 25 | 25 |
| *Percentage* | .. | .. | *56* | .. | *100* |
| *Aphis medicaginis* reared on California privet: | | | | | |
| Lot 1 | 2 | 5 | 4 | 5 | 5 |
| Lot 2 | 2 | 5 | 2 | 5 | 4 |
| Lot 3 | 2 | 5 | 2 | 5 | 5 |
| Lot 4 | 2 | 5 | 2 | 5 | 4 |
| Lot 5 | 2 | 5 | 1 | 5 | 4 |
| Total | .. | 25 | 11 | 25 | 22 |
| *Percentage* | .. | .. | *44* | .. | *88* |

* 20 aphids per lot.

† Virus extract for mechanical inoculation was taken from the same diseased beet on which the corresponding lot of aphids fed.

TABLE 7—*Continued*

| Aphid species, plant it was reared on, and lot* no. | Aphid transmission: Period on diseased beet, days | Aphid transmission: Beets inoculated | Aphid transmission: Beets infected | Mechanical inoculation†: Beets inoculated | Mechanical inoculation†: Beets infected |
|---|---|---|---|---|---|
| *Aphis pomi* reared on *Rumex crispus:* | | | | | |
| Lot 1 | 1 | 5 | 3 | 5 | 4 |
| Lot 2 | 1 | 5 | 1 | 5 | 5 |
| Lot 3 | 1 | 5 | 1 | 5 | 5 |
| Lot 4 | 1 | 5 | 0 | 5 | 5 |
| Lot 5 | 1 | 5 | 0 | 5 | 5 |
| Total | .. | 25 | 5 | 25 | 24 |
| *Percentage* | .. | .. | *20* | .. | *96* |
| *Cavariella capreae* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 1 | 5 | 4 |
| Lot 2 | 2 | 5 | 1 | 5 | 5 |
| Lot 3 | 2 | 5 | 0 | 5 | 5 |
| Lot 4 | 2 | 5 | 0 | 5 | 5 |
| Lot 5 | 2 | 5 | 0 | 5 | 4 |
| Total | .. | 25 | 2 | 25 | 23 |
| *Percentage* | .. | .. | *8* | .. | *92* |
| *Myzus solani* reared on celery: | | | | | |
| Lot 1 | 2 | 5 | 4 | 5 | 5 |
| Lot 2 | 2 | 5 | 2 | 5 | 5 |
| Lot 3 | 2 | 5 | 2 | 5 | 5 |
| Lot 4 | 2 | 5 | 2 | 5 | 5 |
| Lot 5 | 2 | 5 | 1 | 5 | 4 |
| Total | .. | 25 | 11 | 25 | 24 |
| *Percentage* | .. | .. | *44* | .. | *96* |
| *Rhopalosiphum conii* reared on *Conium maculatum:* | | | | | |
| Lot 1 | 1 | 5 | 2 | 5 | 4 |
| Lot 2 | 1 | 5 | 1 | 5 | 5 |
| Lot 3 | 1 | 5 | 1 | 5 | 5 |
| Lot 4 | 1 | 5 | 1 | 5 | 5 |
| Lot 5 | 1 | 5 | 0 | 5 | 5 |
| Total | .. | 25 | 5 | 25 | 24 |
| *Percentage* | .. | .. | *20* | .. | *96* |
| *Rhopalosiphum pseudobrassicae* reared on stock: | | | | | |
| Lot 1 | 1 | 5 | 2 | 5 | 5 |
| Lot 2 | 1 | 5 | 1 | 5 | 5 |
| Lot 3 | 1 | 5 | 0 | 5 | 5 |
| Lot 4 | 1 | 5 | 0 | 5 | 5 |
| Lot 5 | 1 | 5 | 0 | 5 | 5 |
| Total | .. | 25 | 3 | 25 | 25 |
| *Percentage* | .. | .. | *12* | .. | *100* |

* 20 aphids per lot.

† Virus extract for mechanical inoculation was taken from the same diseased beet on which the corresponding lot of aphids fed.

reared on other host plants, was compared with mechanical inoculations. Previously noninfective aphids were fed on 5 infected beets from 24 to 48 hours, then were transferred in lots of 20 to each of 5 healthy beets. The virus extract from each infected plant on which the aphids had fed was inoculated into 5 healthy beets. The aphids that transmitted the virus were:

Celery leaf aphid, *Aphis apigraveolens* Essig
Celery aphid, *Aphis apii* Theobald[7]
Rusty-banded aphid, *Aphis ferruginea-striata* Essig
Cotton or melon aphid, *Aphis gossypii* Glover
Bur clover or cowpea aphid, *Aphis medicaginis* Koch
Green apple aphid, *Aphis pomi* De Geer
Cabbage aphid, *Brevicoryne brassicae* (Linnaeus)
Yellow willow aphid, *Cavariella capreae* (Fabricius)
Turnip or false cabbage aphid, *Rhopalosiphum pseudobrassicae* (Davis)
Foxglove aphid, *Myzus solani* (Kaltenbach)
Honeysuckle aphid, *Rhopalosiphum conii* (Davidson)

As shown in table 7, *Aphis apigraveolens* fed readily on beets and transmitted the virus to 76 per cent of the plants, a higher percentage than that obtained with any of the three species reared on infected beets reported in table 6. The transmission of the virus by *Aphis apii, A. gossypii, A. medicaginis,* and *Myzus solani* was 64, 56, 44, and 44 per cent respectively (table 7). They also fed readily on beets even though reared on other plants.

Essig (1934) stated that *Aphis gossypii* attacks a wide variety of plants, including spinach; and Gillette and Palmer (1931–1934) reported that *A. medicaginis* occurs on *Kochia* in the family Chenopodiaceae. It is not improbable that the species of aphids which have been reported on plants of the Chenopodiaceae other than beets, as well as those species which were observed to feed readily on beets, may play a significant part in spread of the virus in beet fields, or from beets to weeds, and vice versa.

Transmission of the virus by the *Aphis ferruginea-striata, A. pomi, Cavariella capreae, Rhopalosiphum conii,* and *Rhopalosiphum pseudobrassicae* was 8, 20, 8, 20, and 25 per cent respectively (table 7). It was noted, however, that these species did not readily feed on beets and were not inclined to stay long on them. It is possible, therefore, that more infections did not result because few or no aphids fed on the infected or on the healthy beets.

Five trials from each of 20 infected beets, or a total of 100 tests, were made with lots of 20 cabbage aphids, *Brevicoryne brassicae;* 7 beets developed symptoms of the disease.

Twenty-five lots of 20 beet aphids, *Prociphilus betae* (Doane), transferred from the roots of mosaic to healthy beets, failed to transmit the virus.

A summary of the percentages of infections obtained with aphid species reared on mosaic beets and other host plants is shown in table 8.

## MASS INOCULATION

In the opinion of nearly all entomologists and plant pathologists, a single aphid or leafhopper of a lot may cause infection; in other words, one of a group may inject the infective dose of a virus into a plant, and the other insects may play no role in producing the disease.

[7] According to E. O. Essig (personal interview), *Aphis apii* Theobald may be identical with *A. helianthi* Monell.

TABLE 8

SUMMARY OF TRANSMISSION OF SUGAR-BEET-MOSAIC VIRUS BY APHID SPECIES WITH LOTS OF 20 APHIDS IN EACH TEST

| Common and scientific name | Number of beets | | Per cent infected |
|---|---|---|---|
| | Inoculated | Infected | |
| Aphids reared on diseased beets: | | | |
| Erigeron root aphid (*Aphis middletonii*) | 25 | 5 | 20 |
| Pea aphid (*Macrosiphum pisi*) | 25 | 15 | 60 |
| Green peach aphid (*Myzus persicae*) | 50 | 28 | 58 |
| Aphids reared on other host plants: | | | |
| Cabbage aphid (*Brevicoryne brassicae*) | 100 | 7 | 7 |
| Celery leaf aphid (*Aphis apigraveolens*) | 25 | 19 | 76 |
| Celery aphid (*Aphis apii*) | 25 | 16 | 64 |
| Rusty-banded aphid (*Aphis ferruginea-striata*) | 25 | 2 | 8 |
| Cotton or melon aphid (*Aphis gossypii*) | 25 | 14 | 56 |
| Bur clover or cowpea aphid (*Aphis medicaginis*) | 25 | 11 | 44 |
| Green apple aphid (*Aphis pomi*) | 25 | 5 | 20 |
| Yellow willow aphid (*Cavariella capreae*) | 25 | 2 | 8 |
| Foxglove aphid (*Myzus solani*) | 25 | 11 | 44 |
| Honeysuckle aphid (*Rhopalosiphum conii*) | 25 | 5 | 20 |
| Turnip or false cabbage aphid *Rhopalosiphum pseudobrassicae*) | 25 | 3 | 12 |

TABLE 9

TRANSMISSION OF SUGAR-BEET-MOSAIC VIRUS BY LOTS OF VARYING NUMBERS OF *MYZUS PERSICAE* TRANSFERRED FROM MOSAIC TO HEALTHY BEETS

| Number of aphids in each lot | Number of lots on each diseased beet | Number of beets | | Per cent infected |
|---|---|---|---|---|
| | | Inoculated | Infected | |
| Test 1: 10 lots of each number from each of 5 diseased beets | | | | |
| 1 aphid | 10 | 50 | 0 | 0 |
| 5 aphids | 10 | 50 | 3 | 6 |
| 10 aphids | 10 | 50 | 10 | 20 |
| 20 aphids | 10 | 50 | 18 | 36 |
| 40 aphids | 10 | 50 | 37 | 74 |
| Test 2: 5 lots of each number from each of 10 diseased beets | | | | |
| 1 aphid | 5 | 50 | 2 | 4 |
| 5 aphids | 5 | 50 | 2 | 4 |
| 10 aphids | 5 | 50 | 4 | 8 |
| 20 aphids | 5 | 50 | 10 | 20 |
| 40 aphids | 5 | 50 | 18 | 36 |

**By Varying Numbers of Aphids.** The green peach aphid, *Myzus persicae*, was chosen in the following experiments because of its readiness in colonizing on sugar beets and facility in handling. Populations of *M. persicae* were reared on 5 experimentally infected beets, from each of these, 10 lots each of 1, 5, 10, 20, and 40 apterous aphids were transferred to healthy beets. The results appear in table 9.

As shown in this table, there was a definite tendency toward an increase in number of infections obtained when the number of aphids was increased. No infections were obtained with 50 single aphids, while 6 per cent resulted with 5 aphids, 20 per cent with 10 aphids, 36 per cent with 20 aphids, and 74 per cent with 40 aphids in each lot.

This experiment was repeated with *Myzus persicae* reared on 10 experimentally infected sugar beets, from each of which 5 lots each of 1, 5, 10, 20,

TABLE 10

SHORT PERIODS OF TRANSMISSION OF SUGAR-BEET-MOSAIC VIRUS BY VARYING NUMBERS OF *MYZUS PERSICAE*

| Number of aphids on each beet | Minutes on infected beet | Minutes on healthy beet | Number of beets | | Per cent infected |
|---|---|---|---|---|---|
| | | | Inoculated | Infected | |
| 3 days after symptoms developed | | | | | |
| 1 | 5 | 5 | 10 | 0 | 0 |
| 2 | 5 | 5 | 10 | 1 | 10 |
| 3 | 5 | 5 | 10 | 3 | 30 |
| 4 | 5 | 5 | 10 | 3 | 30 |
| 5 | 5 | 5 | 10 | 5 | 50 |
| 15 days after symptoms developed | | | | | |
| 1 | 5 | 5 | 10 | 0 | 0 |
| 2 | 5 | 5 | 10 | 4 | 40 |
| 3 | 5 | 5 | 10 | 2 | 20 |
| 4 | 5 | 5 | 10 | 5 | 50 |
| 5 | 5 | 5 | 10 | 4 | 40 |
| Results summarized | | | | | |
| 1 | 5 | 5 | 20 | 0 | 0 |
| 2 | 5 | 5 | 20 | 5 | 25 |
| 3 | 5 | 5 | 20 | 5 | 25 |
| 4 | 5 | 5 | 20 | 8 | 40 |
| 5 | 5 | 5 | 20 | 9 | 45 |

and 40 aphids were transferred to healthy beets. These results also appear in table 9. The percentage of infection increased from 4 per cent with 1 or 5 aphids per plant to 36 per cent with 40 aphids. These results, however, do not prove mass inoculation.

**By Single Aphids in Short Feeding Time.** An experiment was conducted on virus transmission by *Myzus persicae* in short feeding periods on mosaic and healthy beets. Lots of 1, 2, 3, 4, and 5 previously noninfective, mature, apterous aphids were fed for 5 minutes on an infected beet 3 days after symptoms developed, and then on healthy beets for the same length of time. The same procedure was repeated again, 15 days after the first symptom appeared on the same beet.

Table 10 shows that no infections resulted when single aphids were used, and in general, the percentages of infections increased with the number of aphids used. No significant differences were noted between the results obtained

3 days and 15 days after symptoms had developed on the original infected beet. An average of 25 per cent infection was obtained with lots of 2 and 3 aphids, 40 per cent with 4, and 45 per cent with 5 aphids, as shown in the summarized results in table 10. Again there was no evidence to prove mass inoculation in this experiment.

## RETENTION OF VIRUS

An experiment was conducted to determine how long *Myzus persicae* would retain the virus. Lots of 20 previously noninfective aphids were kept 1 hour on 10 different mosaic beets, then each lot was transferred hourly to 8 successive healthy beets, and maintained 15 hours on the ninth healthy beet.

TABLE 11

RETENTION OF SUGAR-BEET-MOSAIC VIRUS BY LOTS OF *MYZUS PERSICAE* TRANSFERRED HOURLY TO SUCCESSIVE HEALTHY SUGAR BEETS

| Lot no. | Number of aphids on first plant | Results* on successive plants, with hourly transfers | | | | | | | | Last infection produced by aphids, hour |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1st | 2d | 3d | 4th | 5th | 6th | 7th | 8th | |
| 1 | 20..... | + | + | − | − | − | − | − | − | 3d |
| 2 | 20..... | + | − | − | − | − | − | − | − | 2d |
| 3 | 20..... | + | − | − | − | − | − | − | − | 2d |
| 4 | 20..... | + | − | − | − | − | − | − | − | 2d |
| 5 | 20..... | + | − | − | − | − | − | − | − | 2d |
| 6 | 20..... | + | − | − | − | − | − | − | − | 2d |
| 7 | 20..... | − | + | − | − | − | − | − | − | 3d |
| 8 | 20..... | − | + | − | − | − | − | − | − | 3d |
| 9 | 20..... | − | + | − | − | − | − | − | − | 3d |
| 10 | 20..... | − | − | + | − | − | − | − | − | 4th |
| | Total +..... | 6 | 4 | 1 | 0 | 0 | 0 | 0 | 0 | .. |
| | Total −..... | 4 | 6 | 9 | 10 | 10 | 10 | 10 | 10 | .. |

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted. Aphids were left 15 hours on the eighth plant.

As table 11 shows, infections occurred in 6 of 10 tests within the first hour, 3 within the second hour, and 1 within the third hour. One lot infected two successive plants during the first and second hours. No transmission of the virus was obtained after the third hour. It is possible, however, that with a lowering of the temperature during the winter, the aphids may retain the infectivity longer than 3 hours under natural conditions.

## LOSS AND RECOVERY OF INFECTIVITY BY APHIDS ON INOCULATED PLANTS

An attempt was made to determine whether *Myzus persicae* was able to recover the virus from infected sugar beets before the first symptom of the disease developed. Large numbers of aphids were transferred from populations reared on 5 experimentally infected beets to 5 large healthy beets for a period of 2 days. From the third to the fourteenth day, lots of 20 of these aphids were transferred from each plant so inoculated to healthy beets.

The loss and recovery of infectivity by aphids on beets which they inocu-

lated with the virus, and the incubation period of the disease, or the period for the first symptom to develop, is shown in table 12. The elapsed time to the first recovery of the virus by aphids from the original infected beet varied from 8 to 12 days. The incubation period of the disease in the original infected beets varied from 8 to 12 days. A comparison of the first recovery of the virus by lots of 20 aphids with the incubation period of the disease in the original infected plants shows that only 1 lot of aphids recovered the virus before symptoms of the disease developed (1 day before), 1 lot recovered the virus on the same day that the first symptom appeared, and 3 lots recovered the virus in from 1 to 2 days after the earliest symptom developed.

TABLE 12

LOSS AND RECOVERY OF INFECTIVITY BY *MYZUS PERSICAE* ON SUGAR BEETS WHICH THEY INOCULATED WITH SUGAR-BEET-MOSAIC VIRUS

| Original plant number | Results* on successive healthy beets, with aphids left 1 day on each beet (20 aphids per lot) | | | | | | | | | | | | Days to the first symptom on original plant |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. 1 (3d day) | No. 2 (4th day) | No. 3 (5th day) | No. 4 (6th day) | No. 5 (7th day) | No. 6 (8th day) | No. 7 (9th day) | No. 8 (10th day) | No. 9 (11th day) | No. 10 (12th day) | No. 11 (13th day) | No. 12 (14th day) | |
| 1 | − | − | − | − | − | + | − | + | + | + | − | + | 9 |
| 2 | − | − | − | − | − | − | + | + | − | + | − | + | 8 |
| 3 | − | − | − | − | − | − | − | + | + | − | + | + | 9 |
| 4 | − | − | − | − | − | − | − | + | − | − | + | − | 8 |
| 5 | − | − | − | − | − | − | − | − | − | + | + | − | 12 |
| Total + | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 4 | 2 | 3 | 3 | 3 | |
| Total − | 5 | 5 | 5 | 5 | 5 | 4 | 4 | 1 | 3 | 2 | 2 | 2 | |

* The plus sign (+) indicates the production of the disease, and the minus sign (−) shows that no disease resulted.

## ATTEMPT TO TRANSMIT VIRUS WITH CORNICLE EXUDATE

No Malpighian tubules are known to occur in any species of aphids, and some of the waste products are probably eliminated in the cornicle exudate. Extensive tests were made to determine whether the cornicle exudate from infective *Myzus persicae,* possibly containing the virus, would cause the disease. Infective aphids were reared on a mosaic beet; each was touched gently on the abdomen with the point of a needle, and the cornicle exudate excreted was inoculated into the petioles, midrib, or veins of healthy beet seedlings. Five leaves of each beet were inoculated, each with one droplet from a different aphid. Fifty beet seedlings inoculated remained healthy.

## SEPARATION OF MULTIPLE VIRUSES

Sugar beets showing symptoms of both mosaic and curly top on the same plant are common in the field, especially when outbreaks of aphids and the beet leafhopper, *Eutettix tenellus* (Baker), occur. When previously noninfective *Myzus persicae* and the beet leafhopper were exposed to a sugar beet containing the two viruses, *M. persicae* transmitted only the mosaic virus and the beet leafhopper only the curly-top virus to healthy sugar beets, as reported

in a previous paper (Severin, 1929). The two viruses thus were separated from a virus complex.

When the expressed juice from the leaves of a sugar beet containing the two viruses is inoculated into healthy sugar beets, an infection of only beet mosaic occurs by mechanical inoculation with the carborundum method. However, in an experiment previously reported (Severin, 1924), curly-top infection occurred with 9 out of 100 healthy beets when the virus extract from curly-top beets was inoculated into the crown with a flamed needle.

## DESCRIPTION OF VIRUS

**Name**: Sugar-beet mosaic.

**Host families**: Chenopodiaceae, Aizoaceae, and Solanaceae.

**Symptoms of disease**: minute yellow or pale-green flecks, followed by vein clearing on youngest leaves, mottling followed by chlorosis, chlorotic rings with green centers on intermediate leaves, rarely deep-green blisterlike elevations, stunting of young plants, sometimes necrosis of petioles, midrib, and lateral veins under natural conditions.

**Incubation period of disease**: average 25.2 days outdoors during the autumn.

**Properties of virus**: thermal inactivation 60°C in 10-minute exposures; tolerance to dilution 1 : 5,000; resistance to aging *in vitro* 6 days.

**Modes of transmission**: Mechanical inoculation with expressed juice, 4 aphid species reared on sugar beets, 11 aphid species reared on other host plants.

## LITERATURE CITED

BÖNING, K.
1927*a*. Die Mosaikkrankheit der Rübe. Zeitschr. f. Pflanzenkrankh. **37**:19–25. *Abstracted in:* Rev. Appl. Mycol. **6**:330–31; 1927.
1927*b*. Die Mosaikkrankheit der Rübe. Forsch. auf dem Geb. Pflanzenkrankh. u. Immunität im Pflanzenr. **3**:81–128. *Abstracted in:* Rev. Appl. Mycol. **6**:591–92; 1927.
1927*c*. Über die wechselseitige Übertragbarkeit der Mosaikkrankheiten von Rübe und Spinat. Centralbl. f. Bakt. [etc.] Abt. II **71**:490–97. *Abstracted in:* Biol. Abs. **2**:855 (item 9305); 1928.

BORYSSEWICZ, G.
1930. The mosaic of the leaves of the sugar beet. English summary p. 158–60. *In:* Muraviov (1930).

BRANDENBURG, E.
1927. Die Mosaikkrankheit (Gelbfleckigheit) des Spinats und ihre Uebertragung durch Insekten. Ztschr. f. Pflanzenkrank. **37**:173–82. *Abstracted in:* U. S. Off. Expt. Stas., Exp. Sta. Rec. **59**:543; 1928.

CONNERS, I. L.
1935. Fourteenth annual report of the Canadian plant disease survey 1934. 116 p. (See especially p. 23.) Canada Dept. Agr., Experimental Farms Branch, Ottawa, Canada. (Mimeo.)

DE HAAN, K., and G. ROLAND.
1935. Enquête internationale sur les différents types de maladies de jaunissement et de mosaïque de la betterave sucrière quant à leurs caractères et à leur influence sur la végétation. Inst. Belge pour l'Amélioration de la Betterave Pubs. **3**(2):55–67. *Abstracted in:* Rev. Appl. Mycol. **14**:549; 1935.

DUCOMET, V.
1928. La mosaïque de la betterave. Rev. Path. Veg. et Ent. Agr. **15**:24–29. *Abstracted in:* Rev. Appl. Mycol. **7**:418–19; 1928.
1929. La mosaïque de la betterave et la selection. Assoc. Internat. Sélectionneurs de Plantes de Grande Cult., Gembloux, Bul. **2**:44–48. *Abstracted in:* Rev. Appl. Mycol. **9**:620; 1930.

ERIKSSON, J.
1912. Svampsjukdomar a svenska betodlingar. Centralanstalten för Försöksvasendet pa Jordbruksomradet Medel. **66** (Bot. Afd. 3):1–30. *Abstracted in:* Bot. Centbl. **122**(6):148; 1913.

ESAU, KATHERINE.
1944. Anatomical and cytological studies on beet mosaic. Jour. Agr. Res. **69**:95–117.

ESSIG, E. O.
1934. Insects of western North America. xi + 1035 p. (See especially p. 241.) The Macmillan Company, New York, N.Y.

GILLETTE, C. P., and M. A. PALMER.
1931–1934. The Aphidae of Colorado. Ent. Soc. America Ann. **24**:827–934; **25**:369–496; **27**:133–255.

HINO, IWAO.
1933. List of plants susceptible to mosaic and mosaic-like diseases. Miyazaki Col. Agr. and Forestry Bul. **5**:97–111.

HOGGAN, ISMÉ A.
1933. Some viruses affecting spinach, and certain aspects of insect transmission. Phytopathology **23**:446–74.

HOLMES, FRANCIS O.
1939. Handbook of phytopathogenic viruses. 221 p. Burgess Publishing Co., Minneapolis, Minn.

JOHNSON, JAMES, and ISMÉ A. HOGGAN.
1935. A descriptive key for plant viruses. Phytopathology **25**:328–43.

JONES, LEON K.
1931. The mosaic disease of beets. Washington Agr. Exp. Sta. Bul. **250**:1–16.

LIND, J.
1915. Runkelroernes mosaiksyge. Tidsskr. for Planteavl **22**:444–57.

MCKINNEY, H. H.
1944. Genera of the plant viruses. Wash. Acad. Sci. Jour. **34**(5):139–54.

MOLZ, E.
1926. Die Mosaikkrankheit der Zuckerrüben, eine in Deutschland neue und defährliche Zuckerrübenkrankheit. Deut. Landw. Presse **53**:501. *Abstracted in:* Rev. Appl. Mycol. **6**:266; 1927.

MOORE, W. C.
1943. Report on fungus, bacterial, and other diseases of crops in England and Wales. [Gt. Brit.] Min. Agr. and Fisheries Bul. **126**:1–100.

MURAVIOV, V. P. (Editor).
1930. Mosaic diseases of the sugar beet. 286 p. *Papers by Muraviov:* Materials for studying the mosaic of the sugar beet. English summary p. 128–30. To the diagnostic of the mosaical diseases of the sugar beet. English summary p. 138–40. General sketch of mosaic diseases of sugar beet. English translation p. 223–61. Plant Breeding Department of the Union Sugar Concern, Kiev, U.S.S.R. *Abstracted in:* Rev. Appl. Mycol. **11**:89–91.

NOVINENKO, A. J.
1930. The insects as transmitters of mosaic diseases of the sugar beet. English summary p. 111. *In:* Muraviov (1930).

OGILVIE, LAURENCE.
1942. Diseases of vegetables. [Gt. Brit.] Min. Agr. and Fisheries Bul. **123**:1–84.

PETHERBRIDGE, F. R., and H. H. STIRRUP.
1935. Pests and diseases of the sugar-beet. [Gt. Brit.] Min. Agr. and Fisheries Bul. **93**:1–58.

POUND, G. S.
1947. Beet mosaic in the Pacific Northwest. Jour. Agr. Res. **75**:31–41.

PRILLIEUX, E., and G. DELACROIX.
1898. La jaunisse, maladie bacterienne de la betterave. [Paris] Acad. des Sci. Compt. Rend. **127**:338–39. *Abstracted in:* U. S. Off. Expt. Stas., Expt. Sta. Rec. **10**:649; 1898–99.

PROIDA, P. A.
1930. Mosaic of the sugar beet. English summary p. 64–66. *In:* Muraviov (1930).

QUANJER, H. M.
1936. Historique des recherches sur la jaunisse et la mosaïque de la betterave. Inst. Belge pour l'Amelior. de la Betterave Pubs. **4**(2):23–33.

QUANJER, H. M., and G. ROLAND.
1936. De vergelingsziekte en de mozaiekziekte van suiker- en voederbiet. I. Quanjer, H. M. Geschiedenis van het onderzoek over de vergelingsziekte en de mozaiekziekte van de biet. II. Onderzoek van de vergelingsziekte van de biet, met enkele opmerkingen over de mozaiekziekte. [Virus yellows and mosaic disease of sugar and fodder beet. I. History of the investigation on virus yellows and mosaic. II. Investigation on virus yellows and some remarks on mosaic.] Tijdschr. over Plantenziekten **42**:45–70. English summary. *Abstracted in:* Rev. Appl. Mycol. **15**:548–49; 1936.

RAWLINS, T. E., and C. M. TOMPKINS.
1936. Studies on the effect of carborundum as an abrasive in plant virus inoculations. Phytopathology **26**:578–87.

ROBBINS, W. W.
1921. Mosaic disease of sugar beets. Phytopathology **11**:349–65.

ROLAND, G.
1936. Recherches sur la jaunisse de la betterave et quelques observations sur la mosaïque de cette plante. Inst. Belge pour l'Amelior. de la Betterave Pubs. **4**(2): 13–35 (reprint pagination).

ROSTRUP, E.
1904. Oversigt over Landbrugsplanternes Sygdomme. Tidsskr. for Landbrugets Planteavl. **11**:395–424.

SCHAFFNIT, E., and H. WEBER.
1927. Über das Vorkommen von intrazellularen Körpern in den Geweben mosaikkranker Rüben. Forsch. auf dem Geb. der Pflanzenkrank. u. Immunität im Pflanzenr. **4**:23–42. *Abstracted in:* Rev. Appl. Mycol. **7**:108–9; 1928; *and* Biol. Abs. **4**:2238 (item 23771); 1930.

SCHMIDT, E. W.
1927. Zur Mosaikkrankheit der Zuckerrübe. Deutsch. Bot. Gesell. Ber. **45**:598–601. *Abstracted in:* Rev. Appl. Mycol. **7**:355; 1928.
1935. Bericht über neuere Arbeiten zur Biologie der Zuckerrübe. Deutsch. Zuckerindustr. **60**:864–66, 901–2. *Abstracted in:* Rev. Appl. Mycol. **15**:193; 1936.

SEVERIN, H. H. P.
1924. Curly leaf transmission experiments. Phytopathology **14**(2):80–93.
1929. Curly top symptoms on the sugar beet. California Agr. Exp. Sta. Bul. **465**:1–35.
1930. Life-history of beet leafhopper, *Eutettix tenellus* (Baker) in California. Univ. California Pubs. Ent. **5**:37–88.
1948. Additional virus diseases of spinach in California. Hilgardia. **18**(14):531–38.

SEVERIN, H. H. P., and R. M. DRAKE.
1947. Weeds experimentally infected with sugar-beet-mosaic virus. Hilgardia **17**(17): 567–76.

SHEVTSHENKO, I. S.
1930. Report of the mosaic-disease of the sugar beet at the phytopathological section of the Kharkov Regional Agricultural Experiment Station for 1928–1929. English summary p. 97–98. To the question about the injury, which produces the mosaic on the sugar beet. English summary p. 166. *In:* Muraviov (1930).

SMITH, K. M.
1933. Recent advances in the study of plant viruses. 423 p. J. & A. Churchill, London.
1934. The mosaic disease of sugar-beet and related plants. [Gt. Brit.] Agr. Jour. **41**: 269–74.
1937. A textbook of plant virus diseases. 615 p. P. Blakiston's Son & Co. Inc., Philadelphia, Pa.

TOWNSEND, C. O.
1915. Sugar-beet mosaic. Science n.s. **42**:219–20.

VAN DER MEULEN, J. G. J.
1928. Voorloopig onderzoek naar de specialisatie en de infectiebronnen der mosaiekziekten van landbouwgewassen. [Preliminary investigation on the specialization and the sources of infection of mosaic diseases of some agricultural crops.] With an introduction by H. M. Quanjer. English summary, p. 95–96. Landbouw [Buitenzorg, Java] **4**:63–96. *Published also in:* Tijdschr. over Plantenziekten **34**:155–76. *Abstracted in:* Rev. Appl. Mycol. **7**:658–59.

VERPLANCKE, G.
1933. Les viroses de la betterave. Sucr. Belge **53**:2–10, 22–32. *Abstracted in:* Rev. Appl. Mycol. **13**:210–11; 1934.
1934. Contribution a l'étude des maladies à virus filtrants de la betterave. Brussels Acad. Roy. de Belg. Mém. 2d ser. **13**:1–104.
1934–35. Étude des propriétés des virus causant les maladies de dégénerescence de la betterave. Sucr. Belge **54**:118–27, 142–51, 162–68.

WATSON, M. A.
1936. Factors affecting the amount of infection obtained by aphis transmission of the virus Hy. III. Roy. Soc. London, Philos. Trans., Ser. B, **226**:457–89.

WATSON, M. A., and F. M. ROBERTS.
1939. A comparative study of the transmission of *Hyoscyamus* virus 3, potato virus Y, and cucumber virus I, by the vectors *Myzus persicae* (Sulz.), *M. circumflexus* (Buckton), and *Macrosiphum gei* (Koch). Roy. Soc. London Proc., Ser. B, **127**: 543–76.

## APPENDIX TO CITATIONS

Brief notes of the occurrences of sugar-beet mosaic in the United States have appeared in the Plant Disease Reporter.[8] Frequently the collaborators of these reports were not mentioned, and it was found more convenient to list them in the chronological order rather than under the name of the collaborators and editors.

1921*a*. The Plant Disease Reporter **5**(9):139.
1921*b*. The Plant Disease Reporter Suppl. **16**:265–66.
1923. The Plant Disease Reporter Suppl. **26**:134.
1926. The Plant Disease Reporter Suppl. **45**:141.
1927. The Plant Disease Reporter **11**(4):42.
1928*a*. The Plant Disease Reporter Suppl. **59**:85.
1928*b*. The Plant Disease Reporter Suppl. **61**:294.
1929. The Plant Disease Reporter Suppl. **68**:108.
1930*a*. The Plant Disease Reporter **14**(17):176.
1930*b*. The Plant Disease Reporter Suppl. **75**:55–56.
1936. The Plant Disease Reporter **20**(15):231.
1943. The Plant Disease Reporter **28**(36):643.
1944. The Plant Disease Reporter **28**(36):1095–96.

[8] A mimeographed pamphlet issued by the United States Bureau of Plant Industry.

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