APHID TRANSMISSION OF THREE STRAINS OF CUCUMBER MOSAIC VIRUS

by

ROBERT LEROY NELSON

A THESIS

submitted to

OREGON STATE COLLEGE

in partial fulfillment of
the requirements for the
degree of

MASTER OF SCIENCE

June 1959

APPROVED:

Redacted for Privacy

Associate Professor of Entomology

In Charge of Major

Redacted for Privacy

Chairman of Department of Entomology

Redacted for Privacy

Chairman of School Graduate Committee

Redacted for Privacy

Dean of Graduate School

Date thesis is presented August 14, 1958

Typed by Lucy Korten

ACKNOWLEDGEMENTS

The writer is greatly indebted to Dr. Knud G. Swenson, Associate Professor of Entomology, through whose willing help and guidance the investigations reported in this thesis were completed. He is also grateful to Dr. John A. Milbrath, Professor of Plant Pathology, who advised on matters concerning plant viruses and provided viruses used in the work carried out. The writer additionally wishes to thank the members of the Department of Entomology and friends, who aided in many ways, and his wife, Shannon, who provided constant encouragement and assistance, throughout the course of the investigations.

TABLE OF CONTENTS

LIST OF TABLES

APHID TRANSMISSION OF THREE STRAINS OF CUCUMBER MOSAIC VIRUS

INTRODUCTION

Cucumber mosaic virus exists as a number of strains which, individually and collectively, infect a wide variety of plants. In 1940 Price (72, p. 540) reported that one strain of this virus infected 191 species of plants representing 40 families. According to Faan and Johnson (30, p. 1001), approximately 200 species of plants were known to be hosts of this virus by 1950.

Many plant diseases, including some of great economic importance, result from the activity of cucumber mosaic virus in its many host plants. Among the important diseases caused by the virus are cucumber mosaic, spinach blight and southern celery mosaic.

One of the most damaging diseases associated with this virus in Oregon is known as white break of gladiolus. In 1956 Snow (94, p. 2) stated that "with respect to gladiolus production in the Portland area, the most serious virus disease has been due to cucumber mosaic virus. This virus alone, or in combination with other viruses, is responsible for the flower breaking and noticeable white streaking and flecking of foliage that is associated with the disease known as white break." Reports of the occurrence of cucumber mosaic virus in the gladiolus

are briefly reviewed in the appendix.

Numerous reports relating to the transmission of cucumber mosaic virus by insects, particularly aphids, have been made. Because of their number, and because of confusion existing in aphid and plant virus nomenclature and classification, these reports have been difficult to appraise.

In seeking information concerning the natural spread of the white break disease, it was desirable to determine whether cucumber mosaic virus is likely to be transmitted by few or many species of aphids. The investigations described in this thesis were carried out primarily to acquire this information. In addition, reports of insect transmission of cucumber mosaic virus are extensively reviewed in an attempt to clarify the situation in respect to such transmission, as well as because such reports have a direct bearing on the work herein reported.

All scientific names of insects appearing in the review are names of aphids, unless otherwise noted. In many cases the names of aphids, as given in the reports reviewed, differ from the names for those aphids preferred in America, as presented by Dickson (20) in 1955. In such cases in the review, the preferred American names are given, in parentheses, following the reported names. Occasionally names of aphids are given for which no preferred American names are available.

REVIEW OF LITERATURE

Probably the first report implicating aphids as vectors of cucumber mosaic virus was also the first report of aphid transmission of a plant virus. It was stated in this report, by Allard (3, p. 27) in 1914, that "the occurrence of the mosaic disease in tobacco plants... was unquestionably associated with infestation of the plants by aphides of the species Macrosiphum tabaci Pergande." This report, according to Smith and Brierley (87, p. 300), "has been difficult to evaluate because the identity of his (Allard's) vector, Macrosiphum tabaci Perg., was uncertain and also because aphids have failed to transmit the tobacco mosaic virus from tobacco to tobacco in more recent experiments." These workers also stated (87, p. 301) that "it is probable that in Allard's experiment the cucumber mosaic virus was transmitted from tobacco to tobacco by Macrosiphum solanifolii (Ashmead)."

In a later paper on the mosaic disease of tobacco (2, p. 626-629) Allard related that both Macrosiphum tabaci and Myzus persicae (Sulzer) may become active carriers of the infective principle of the disease and indicated that Macrosiphum lactucae Kaltenbach and Macrosiphum pelargonii (Kalt.) are unable to carry it. He also reported (2, p. 629) that whiteflies, Aleyrodes vaporariorum Westwood, and red spiders, Tetranychus telarius Linnaeus, do not appear

to be actively concerned with the spread of the disease.

That Myzus persicae readily transmits cucumber mosaic virus between tobacco and certain other solanaceous hosts has been demonstrated by Hoggan (45, p. 121) (42, p. 211). In addition, Hoggan has shown (44, p. 21) (42, p. 211) that Myzus pseudosolani Theobald (M. solani (Kalt.)), Myzus circumflexus (Buckton) and Macrosiphum solanifolii can transmit the virus from tobacco and tomato to solanaceous hosts.

Apparently the first reports of aphid transmission of cucumber mosaic virus as such were made independently by Doolittle and Jagger in 1916. These workers found (22, p. 146) (49, p. 149) that the cotton or melon aphid, Aphis gossypii Glover, transmitted the virus. This aphid was also reported as a vector of the virus in later papers by Doolittle (24, p. 43-44), Doolittle and Walker (28, p. 43) (27, p. 46) (26, p. 143) and Walker (98, p. 743).

Doolittle (24, p. 44-46) and Doolittle and Walker (27, p. 56) related that the striped cucumber beetle, Diabrotica vittata Fabricius, and the twelve-spotted cucumber beetle, Diabrotica duodecimpunctata Olivier, could transmit cucumber mosaic virus. Doolittle (24, p. 46-47) was unable to transmit the virus with the tarnished plant bug, Lygus pratensis Linn., or with bees, which were thought to possibly be able to carry the virus between blossoms of cucumber plants.

Freitag (32, p. 80), in 1956, could not transmit several strains of cucumber mosaic virus to squash using the western striped cucumber beetle, Acalymma trivittata (Mannerheim), and the western twelve-spotted cucumber beetle, Diabrotica undecimpunctata undecimpunctata Mann. He stated (32, p. 73) that the reports of beetle transmission of cucumber mosaic virus need to be substantiated.

In 1925 Elmer (29, p. 87) reported transmission of the virus(es) causing mosaics of a number of different species of plants, including Cucumis sativus Linn.(cucumber), by several species of insects. He did not consider mosaics of the different species of plants to be caused by different viruses, as some of them probably were. How cucumber mosaic virus may have been involved in Elmer's work consequently seems indefinite.

In 1938 Watson (99, p. 306) transmitted two strains of cucumber mosaic virus using Myzus persicae and Myzus circumflexus. Later Watson and Roberts (100, p. 574) transmitted these viruses with the same two species and with Macrosiphum gei (Koch) (M. solanifolii) as well.

Chamberlain (17, p. 80), in 1939, was able to transmit cucumber mosaic virus with Aphis gossypii, Myzus persicae and Macrosiphum solani Kalt. (Myzus solani (Kalt.)) but not with Macrosiphum solanifolii. Doncaster and Kassanis (21, p. 67) transmitted the virus using Myzus ascalonicus Doncaster and Myzus persicae in 1946 and,

the following year, Kassanis (51, p. 420) found that Myzus ornatus Laing could readily transmit the virus to lettuce.

In 1948 Nienow (65, p. 62) reported transmission of a strain of cucumber mosaic virus from Mertensia virginica (Linn.) between tobacco plants by Myzus persicae, and the same year Chamberlain (19, p. 259) reported that cucumber mosaic virus was transmitted from infected to healthy tree tomatoes, Cyphomandra betacea Sendtner, by the same species of aphid.

In 1957 Semal (76, p. 446) related that cucumber mosaic virus could be transmitted to beets by Myzus ascalonicus and Simons (85, p. 145) transmitted three strains of the virus affecting pepper using Aphis gossypii and Myzus persicae.

A disease of banana known as banana heart rot or infectious chlorosis is thought to be caused by cucumber mosaic virus. Magee (55, p. 929) stated in 1930 that Pentalonia nigronervosa (Coquerel) may transmit the virus causing this disease. He later found (56, p. 481-482) that Macrosiphum gei (M. solanifolii), Aphis gossypii and an unidentified aphid could transmit the virus.

A virus causing mosaic of abacá, Musa textilis Née, in the Philippine Islands has been regarded as identical with cucumber mosaic virus (16, p. 399). In 1954, however, Kent (52, p. 563-564) stated that the mosaic disease of abacá is undoubtedly a complex in which at least five

viruses are concerned, including those causing true abacá mosaic, corn mosaic, sugarcane mosaic, canna mosaic and grass mosaic. Reports concerning aphid transmission of viruses in this complex are thoroughly reviewed by Kent (52, p. 564-566).

Poole (70, p. 152-153), in 1922, demonstrated that the virus causing a celery mosaic could be transmitted to healthy plants by Myzus persicae from diseased plants. Shortly thereafter Elmer, in work previously discussed (29, p. 70), found that the virus causing "mosaic" could be transmitted by Aphis gossypii from mosaic-infected celery to cucumbers.

Doolittle (23, p. 114) thought that a celery mosaic with which he was working in 1931 might be caused by cucumber mosaic virus and stated that the virus causing this mosaic infected creeping dayflower, Commelina nudiflora Linn., and could be transmitted therefrom to celery and cucumber by Aphis gossypii.

Doolittle and Wellman (25, p. 48-61), in 1934, apparently working with the same celery mosaic, found that Aphis gossypii was an able vector of the virus causing it. They were unable to transmit the virus from celery to celery using the celery leaf tyer, Phlyctaenia rubigalis Guenee, the garden flea hopper, Halticus citri Ashm., Lygus pratensis, or the celery looper, Autographa falcifera Kirby (25, p. 53-54).

Later the same year Wellman (102, p. 724) named the virus causing this mosaic "celery virus 1" and the disease caused by the virus "southern celery mosaic". He reported transmission of the virus from creeping dayflower to banana and other plants by Aphis maidis Fitch (Rhopalosiphum maidis (Fitch)) and Aphis gossypii (101, p. 1032) and from creeping dayflower and celery to maize and other Gramineae by the latter aphid (103, p. 1035). Wellman (102, p. 723-724) did not believe this celery virus was a strain of cucumber mosaic virus, which it is now considered to be, but did think that the diseases of Poole and Elmer were caused by cucumber mosaic virus. He later showed (104), by extensive tests, that the southern celery mosaic virus could be transmitted to and from a great many plants, including ornamentals, vegetables and weeds, by Aphis gossypii.

In addition, Carter (15, p. 157), in 1937, reported transmission of a Commelina nudiflora mosaic to pineapple by Aphis gossypii, Myzus persicae and Macrosiphum solanifolii, and Simons (84, p. 217), in 1955, related that southern cucumber mosaic virus, identical with the southern celery mosaic virus, was transmitted by Aphis gossypii, Myzus persicae and Aphis rumicis Linn.(A. fabae Scopoli) in that order of efficiency.

Other reports of aphid transmission of viruses causing celery mosaics, presumably strains of cucumber mosaic

virus, have been made by Gigante (34, p. 227-228) in 1936, and Roland (75, p. 264), in 1951, who designated Cavariella pastinaceae (Linn.) and Myzus persicae, respectively, as vectors.

Semal (77, p. 446) reported in 1956 that a chrysanthemum strain of cucumber mosaic virus infecting celery was transmitted from infected to healthy plants by Myzus persicae but not by Myzus ascalonicus or Aphis gossypii.

Another disease of celery caused by a cucumber mosaic virus is that known in California as celery calico. The celery calico virus has, according to Severin, been transmitted from celery to delphinium seedlings by Aphis apigraveolens Essig, Aphis apii Theob., Aphis ferruginea-striata Essig (A. inculta Walker), Aphis middeltonii (Thomas) (A. armoraciae Cowen), Myzus persicae, Myzus circumflexus, Myzus convolvuli (Kalt.) (M. solani), Aphis gossypii and Rhopalosiphum melliferum Hottes (R. conii (Davidson)) (79, p. 453), from celery to pansies and violas by the first five of these species and Cavariella capreae (Fabr.) (C. aegopodii (Scop.)) and Rhopalosiphum conii (81, p. 586), and from pansies, violas and celery to pansies and violas by Aphis gossypii, Myzus circumflexus, Myzus solani and Micromyzus violae (Perg.) (81, p. 585).

Another strain of cucumber mosaic virus, western cucumber mosaic virus, was said to be transmitted by Aphis gossypii, Aphis rumicis (A. fabae) and Myzus persicae by

Severin (81, p. 586) and Severin and Freitag (83, p. 529). Myzus persicae is considered the principal vector of this virus and of celery calico virus in the field although Aphis rumicis (A. fabae) may occasionally be implicated in their transmission, according to Severin (78, p. 553). Freitag (31, p. 8) stated that 10 species of aphids, which he did not name, readily transmitted western cucumber mosaic virus and that the virus was transmitted to one of 61 squash plants by Acalymma trivittata and to none of 30 such plants by Diabrotica undecimpunctata undecimpunctata.

McClintock and Smith, in 1918, found that the virus causing spinach blight, also considered to be a strain of cucumber mosaic virus, was commonly spread from blighted to healthy spinach by Macrosiphum solanifolii and Rhopalosiphum persicae Sulzer (Myzus persicae) (59, p. 57-58) and less commonly by Aphis rumicis (A. fabae)(59, p. 51). They also reported (59, p. 51) that Lygus pratensis transmitted the virus and that the southern corn rootworm (adults), Diabrotica 12-punctata Oliv., the stink bugs, Nezara hilaris Say and Euchistus servus Say, the thrips, Thrips tabaci Lindeman, and the springtails, Smynthurus hortensis Fitch and Smynthurus quadrimaculatus Ryder, were unable to transmit it.

Hoggan (46, p. 103) (43, p. 459) related that cucumber mosaic virus could be readily transmitted to and from

various plants, including spinach plants, by Myzus persicae and Macrosiphum solanifolii.

Smith (91, p. 110-115) listed Macrosiphum pisi (Kalt.), Aphis rumicis (A. fabae), Macrosiphum gei (M. solanifolii) and Myzus persicae as vectors of spinach blight in 1934 and the last three of these species were also said to be vectors of the blight by Parris in 1938 (69, p. 59).

In 1955 a strain of cucumber mosaic virus infecting spinach was said by Behr (4, p. 426) to be transmitted by Myzodes persicae (Sulzer) (Myzus persicae).

Strains of cucumber mosaic virus from spinach, Primula obconica Hance, and turnip and a derivative of one of Price's yellow strains of cucumber mosaic virus (73) were transmitted by Myzus persicae, Myzus ornatus and Macrosiphum euphorbiae (Thomas) (M. solanifolii) in that order of efficiency, according to Bhargava in 1951 (7, p. 385-387).

In 1935 Smith (90) described a mosaic of Primula obconica which he thought was caused by a virus similar to, if not identical with, cucumber mosaic virus. Tompkins and Middelton (95, p. 678) described a mosaic of this plant in 1941 and failed to transmit the virus causing it with Myzus persicae and Myzus circumflexus. They believed this mosaic was different from Smith's mosaic and from mosaics caused in primula by strains of cucumber mosaic virus with which it was compared. Later Severin

and Tompkins (82, p. 285-286) related that they achieved transmission of this same primula mosaic virus using Myzus circumflexus, Myzus ornatus, Aphis apii, Aphis ferruginea-striata (A. inculta), Aphis gossypii, Aphis rumicis (A. fabae), Brevicoryne brassicae (Linn.), Myzus solani and Macrosiphum pisi.

In addition, Mischke (62, p. 762) recently achieved transmission of a primula mosaic virus using Aphis fabae.

A disease of tomato known as fern leaf is caused in some cases by cucumber mosaic virus and in others by tobacco mosaic virus. Mogendorff (63, p. 44) indicated in 1930 that a virus causing this disease was regularly transferred to tomatoes by Myzus persicae previously fed on plants infected by cucumber mosaic virus. Jones and Burnett (50, p. 8) later stated that Myzus persicae, Macrosiphum gei (M. solanifolii) and Aphis gossypii, as well as the beetles, Diabrotica vittata and Diabrotica 12-punctata, are capable of transmitting the virus causing fern leaf of tomato.

In 1934 Chamberlain (18, p. 262-263) found that the virus causing narrow leaf of tomato, probably cucumber mosaic virus, was transferred from diseased to healthy plants by Myzus pseudosolani (M. solani) but not by Myzus persicae or Macrosiphum gei (M. solanifolii).

Severin (80, p. 115) stated in 1950 that Aphis gossypii, Myzus circumflexus and Myzus persicae can transmit

western cucumber mosaic virus to tomatoes, and Van Koot and Camfferman (96) noted in 1952 that cucumber mosaic virus was evidently transmitted to tomato plants by Macrosiphum euphorbiae (M. solanifolii).

Tomato aspermy virus is apparently the same virus that causes a disease of chrysanthemum known as chrysanthemum aspermy. As pointed out by Smith (92, p. 153), "there is still much confusion existing about the various viruses attacking the chrysanthemum." Smith discusses the possible relationship of chrysanthemum aspermy virus with cucumber mosaic virus (92, p. 157) and states that "evidence suggests that the chrysanthemum virus is related, though perhaps not very closely, to that of cucumber mosaic."

Brierley, Smith and Doolittle (14, p. 404), in 1953, working with a tomato aspermy virus from chrysanthemum, reported transmission of the virus from chrysanthemum to chrysanthemum, tobacco, and tomato, from tobacco to tobacco and tomato, and from tomato to tomato by Myzus persicae, from chrysanthemum to chrysanthemum and tobacco, from tobacco to tobacco, and from tomato to tomato by Myzus solani, from chrysanthemum to chrysanthemum and tobacco by Macrosiphoniella sanborni (Gillette) (Macrosiphum sanborni Gill.), and from chrysanthemum to chrysanthemum by Rhopalosiphum rufomaculatum (Wilson). These workers maintained that the failure of tomato aspermy virus to produce mosaic in cucumbers and fleck in Creole

Easter lily distinguish it from cucumber mosaic virus.

Govier (35, p. 72), however, concluded in 1957 from cross-protection and serological tests that the tomato aspermy virus is a strain of cucumber mosaic virus. He was able to transmit the virus from chrysanthemum to chrysanthemum, tobacco, and tomato by Myzus persicae and Aulacorthum solani (Kalt.) (Myzus solani), from chrysanthemum to chrysanthemum and tobacco by Macrosiphoniella sanborni (Macrosiphum sanborni), from tomato to tomato and tobacco and from tobacco to tobacco by Aulacorthum solani (Myzus solani) and Myzus persicae, and from tomato to tomato by Aphis fabae (35, p. 67). He was not able to transmit the virus using Myzus ascalonicus, Macrosiphum euphorbiae (M. solanifolii), Aulacorthum circumflexum (Buckt.) (Myzus circumflexus) or Nasonovia ribis-nigri (Mosley).

In 1949 Blencowe and Caldwell (8, p. 322-323) were unable to transmit tomato aspermy virus between tomato plants or from tobacco to tomato with Myzus persicae, Aphis fabae, Macrosiphoniella sanborni (Macrosiphum sanborni) or Macrosiphum euphorbiae (M. solanifolii) but could readily transmit it from diseased to healthy tobacco plants with Myzus persicae.

Hollings (47, p. 95), in 1955, reported transmission of the aspermy virus from tobacco to tobacco and from chrysanthemum to chrysanthemum by Macrosiphum euphorbiae

(M. solanifolii), Myzus persicae, Aulacorthum solani (Myzus solani) and Macrosiphoniella sanborni (Macrosiphum sanborni), and from aster to aster and from chrysanthemum to chrysanthemum by Brachycaudus helichrysi (Kalt.)(Aphis helichrysi Kalt.). He was unable to transmit the virus using Myzus ascalonicus, Coloradoa rufomaculata (Wilson) (Rhopalosiphum rufomaculatum (Wilson)) or Aphis rhamni Boyer de Fonscolombe (A. abbreviata Patch).

Wellman, during a study of the host range of southern celery mosaic virus in 1935 (104, p. 387), transmitted the virus to Easter and Golden lilies with Aphis gossypii.

Price (71, p. 568), in 1937, concluded that lily mosaic should be classified in the cucumber mosaic virus group. He said (71, p. 561) that C. E. F. Guterman related in 1930 that mosaic of Easter lily could be transmitted by Aphis gossypii. Guterman and Ogilvie (68, p. 313), the year before, reported that a mosaic of Bermuda Easter lily could not be transmitted by Aphis gossypii, Aphis ogilviei Theob., the leafhoppers, Empoa fabae Harris and Cicadula sexnotata Fall, or by the bulb mite, Rhizoglyphus hyacinthi Banks.

Hopkins (48, p. 448-449) reported in 1941 that Easter lily mosaic was found to be caused by cucumber mosaic virus and that the virus was transmitted from lily to cucumber by Myzus persicae.

In 1944 Brierley and Smith (13, p. 530) gave evidence

that cucumber mosaic virus, plus a virus known as lily symptomless virus, together cause a disease of Easter lily known as necrotic fleck. Aphis gossypii, Macrosiphum solanifolii and Myzus persicae were able to transmit cucumber mosaic virus to lilies, according to these workers, whereas Aphis fabae, Macrosiphum lilii Monell, Myzus circumflexus and Myzus convolvuli (M. solani) failed to do so (13, p. 553). Smith and Brierley, in 1948, found that Myzus persicae readily transmitted the virus from Easter lily to growing plants or sprouts of Creole lily in storage (86, p. 843) and stated (89, p. 851) that, in their experiments covering several years, Myzus convolvuli (M. solani) did not transmit cucumber mosaic virus in lilies.

A disease of passion fruit, Passiflora edulis Sims, often termed passion fruit woodiness, or bullet, disease, is said to be caused by a strain of cucumber mosaic virus. Noble and Noble (66, p. 316) (67, p. 20-21) reported in 1939 that Myzus persicae, Macrosiphum solanifolii, and two dark species belonging to the group in which are included Aphis rumicis (A. fabae) and Aphis medicaginis Koch, were capable of transmitting the passion fruit virus. In 1948 Magee (57, p. 201) stated that this virus can be transmitted by several species of aphids, including Myzus persicae, Macrosiphum solanifolii and Aphis gossypii.

Certain leguminous plants are sometimes infected by

strains of cucumber mosaic virus and such diseases as lima bean mosaic, cowpea mosaic, and browning of lupine result from such infections. The cowpea mosaic caused by cucumber mosaic virus should not be confused with another cowpea mosaic which is transmitted by biting insects (92, p. 218).

Harter (36, p. 901-902), in 1938, transmitted a lima bean mosaic virus, thought to be a strain of cucumber mosaic virus, from diseased to healthy plants with Aphis gossypii and Myzus persicae, and Whipple and Walker (105, p. 41), in 1941, related that two strains of cucumber mosaic virus pathogenic on bean and pea were transmitted by Myzus persicae.

In 1941 McLean (58, p. 423-424) found that the virus causing a cowpea mosaic, apparently a strain of cucumber mosaic virus, was transmitted from diseased to healthy cowpea plants by Macrosiphum solanifolii, Aphis gossypii, Macrosiphum pisi and an unidentified black aphid, resembling Aphis rumicis (A. fabae). He was unable to transmit the virus with Diabrotica vittata, Lygus pratensis, the Mexican flea beetle, Epilachna corrupta Mulsant, or the bean leafhopper, Empoasca fabae Le Baron.

In addition, Yu (106, p. 451) achieved transmission of a cowpea mosaic virus in 1946 using Aphis rumicis (A. fabae), Macrosiphum pisi and Aphis gossypii.

Heinze has reported transmission of cucumber mosaic

virus, which causes browning of lupine in Europe, by a considerable number of species of aphids. In 1939 he (38, p. 84-85) transmitted the virus from lupine to lupine with Myzodes persicae (Myzus persicae), Doralis fabae (Scop.) (Aphis fabae), Doralis frangulae (Koch) (Aphis gossypii), Doralis rhamni (Koch) (Aphis abbreviata), and Aulacorthum solani (Myzus solani) and from cucumber to cucumber by Myzus ornatus. He was unable to transmit the virus with leafhoppers, weevils and psyllids.

The same worker, in 1950 (41, p. 52), reported transmission of cucumber mosaic virus from cucumber to cucumber by Brachycaudus helichrysi (Aphis helichrysi), Brevicoryne brassicae, Hyalopterus arundinis (Fabr.), Doralina urticaria (Kalt.) (Aphis urticata Fabr.), Nasonovia ribicola (Kalt.), Hyperomyzus lactucae (Linn.) (Amphorophora lactucae (Linn.)) and Rhopalosiphoninus latysiphon (David.), from lettuce to lettuce by Dactynotus obscurus (Koch) (Macrosiphum obscurus (Koch)), Hyperomyzus lactucae (Amphorophora lactucae), Neomyzus circumflexus (Buckt.) (Myzus circumflexus (Buckt.) and Macrosiphon solanifolii (Ashm.) (Macrosiphum solanifolii), from calendula to calendula by Coloradoa tanacetina (Kalt.) (Rhopalosiphum tanacetina (Walker)), Brevicoryne brassicae, Brachycaudus helichrysi (Aphis helichrysi), Dactynotus tanaceticola (Kalt.) (Macrosiphum tanaceti (Linn.)) and Myzodes persicae (Myzus persicae), from lupine to lupine by Pergandeida

craccae (Linn.) (Aphis craccae Linn.) and Rhopalosiphoninus latysiphon, and from celery to celery by Anuraphis subterranea (Walker) (Aphis subterranea Walker).

Heinze listed Doralina mordwilkiana (Dobrowljansky) (Aphis mordwilkiana Dobz.) as a vector of the virus from cucumber to cucumber in 1951 (37, p. 52) and, the following year (39, p. 8-9), related that this aphid and Rhopalosiphon nympheae (Linn.) (Rhopalosiphum nympheae (Linn.)), Cryptomyzus ribis (Linn.) (Capitophorus ribis (Linn.)), Myzodes ligustri (Mosley) (Myzus ligustri (Mosley)) and Delphinobium junackianum (Karsch) (Rhopalosiphum junackianum (Karsch)) can transmit the virus between cucumbers, that Pharalis tanaceti (Linn.) (Macrosiphum tanaceti (Linn.)) and Dactynotus tanaceticola (Macrosiphym tanaceti) can transmit it from cucumber to calendula, and that Dysaulacorthum pseudosolani (Theob.) (Myzus solani) and Myzodes persicae (Myzus persicae) can transmit it from cucumber to dahlia.

Recently Heinze (40, p. 24-25) reported transmission of cucumber mosaic virus from cucumber to cucumber by Chaitophorus betulinus van der Goot, Rungsia maydis Passerini, Aphis cirsii-acanthoidis Scop., Cerosipha epilobiina Walker, Metopolophium occidentale Hille Ris Lambers and Metopeurum fuscovirida Stroyan and from Nicotiana glutinosa to cucumber by Megoura viciae Kalt. (Amphorophora viciae (Kalt.)).

A referenced list of the species of aphids reported as vectors of strains, or possible strains, of cucumber mosaic virus is given in the appendix.

MATERIALS AND METHODS

Identification and Handling of Aphids

Each of 13 species of aphids was tested to determine its ability to transmit strains of cucumber mosaic virus.

Most of these aphids were colonized and kept on caged plants in a greenhouse until used in transmission tests. The cages used, primarily of wood frame and fine-mesh screen construction, are illustrated in figure two of a Ph. D. thesis (1) on file in the library at Oregon State College. These cages were placed over the plants and on the rims of six-inch pots or number 10 cans in which they were grown. The cages were never opened in the greenhouse but were taken to a headhouse whenever aphids were to be removed for transferring to new caged host plants or for testing. Any aphids on the external surfaces of the cages were brushed therefrom when the cages were to be returned to the greenhouse. The greenhouse unit in which the aphid cultures were kept was separated from those units in which plants used in tests were kept.

Aphids from six different collections of the bean aphid, Aphis fabae Scopoli, and from seven different collections of the potato aphid, Macrosiphum solanifolii (Ashmead), were tested. The bean aphids were colonized

on broadbean plants, Vicia faba Linnaeus, and the potato aphids, except those collected on potato plants (see collection data in table 1), were colonized on gladiolus plants.

Aphids from single collections of the apple grain aphid, Rhopalosiphum fitchii (Sanderson), the English grain aphid, Macrosiphum granarium (Kirby), the rose grass aphid, Macrosiphum dirhodum (Walker), the cabbage aphid, Brevicoryne brassicae (Linn.), the green peach aphid, Myzus persicae (Sulzer), and the pea aphid, Macrosiphum pisi (Kaltenbach), were tested. Aphids from the first three of these collections were colonized on barley, the cabbage and green peach aphids on broccoli, and the pea aphids on broadbean plants. The green peach and pea aphids were from cultures permanently maintained in the greenhouse.

Some aphids were used in tests immediately after they were collected because they could easily be collected in sufficient numbers for immediate testing and/or could not readily be colonized on plants in the greenhouse. Aphids from single collections of Amphorophora sonchi (Oestlund), Amphorophora rhododendri (Wilson), the rose aphid, Macrosiphum rosae (Linn.), Macrosiphum barri Essig, and the thistle aphid, Aphis cardui Linn., were handled in this manner.

Complete collection data for all of the aphids used

in transmission tests is given in table 1.

TABLE I

COLLECTION DATA FOR APHIDS USED IN TRANSMISSION TESTS

Collection Number	Species	Date	Location	Collected On
1	*Aphis fabae* Scop.	27 Jun 57	Corvallis, Ore.	*Rumex sp.*
2	*Aphis fabae* Scop.	7 Jul 57	Springfield, Ore.	*Rumex sp.*
3	*Aphis fabae* Scop.	7 Jul 57	Springfield, Ore.	*Phaseolus vulgaris*
4	*Aphis fabae* Scop.	9 Jul 57	Gresham, Ore.	*Rumex sp.*
5	*Aphis fabae* Scop.	10 Jul 57	Corvallis, Ore.	*Cucurbita maxima*
6	*Aphis fabae* Scop.	26 Jul 57	Corvallis, Ore.	*Solanum tuberosum*
*7	*Macrosiphum solanifolii* (Ashm.)	24 Jul 57	Corvallis, Ore.	*Gladiolus sp.*
*8	*Macrosiphum solanifolii* (Ashm.)	30 Jul 57	Troutdale, Ore.	*Gladiolus sp.*
*9	*Macrosiphum solanifolii* (Ashm.)	9 Aug 57	Troutdale, Ore.	*Gladiolus sp.*
10	*Macrosiphum solanifolii* (Ashm.)	13 Aug 57	Culver, Ore.	*Solanum tuberosum*
*11	*Macrosiphum solanifolii* (Ashm.)	20 Aug 57	Troutdale, Ore.	*Gladiolus sp.*
*12	*Macrosiphum solanifolii* (Ashm.)	29 Aug 57	Corvallis, Ore.	*Gladiolus sp.*
*13	*Macrosiphum solanifolii* (Ashm.)	6 Nov 57	Corvallis, Ore.	*Iris sp.*
*14	*Rhopalosiphum fitchii* (Sand.)	7 Jan 58	Corvallis, Ore.	*Festuca sp.*
15	*Macrosiphum granarium* (Kirby)	28 Feb 58	Corvallis, Ore.	*Triticum aestivum*

TABLE I Cont'd

Collection Number	Species	Date	Location	Collected On
16	Macrosiphum dirhodum (Walker)	17 Jan 58	Corvallis, Ore.	(unidentified grass)
17	Brevicoryne brassicae (Linn.)	2 Aug 57	Corvallis, Ore.	Brassica caulorapa
18	Myzus persicae (Sulzer)			(stock culture)
19	Macrosiphum pisi (Kalt.)			(stock culture)
*20	Amphorophora sonchi (Oest.)	14 Aug 57	Corvallis, Ore.	Sonchus oleraceus
*21	Amphorophora rhododendri (Wilson)	24 Aug 57	Corvallis, Ore.	Rhododendron sp.
22	Macrosiphum rosae (Linn.)	22 Jul 57	Corvallis, Ore.	Rosa sp.
23	Macrosiphum barri Essig	6 Nov 57	Corvallis, Ore.	Lactuca scariola
24	Aphis cardui Linn.	16 Aug 57	Corvallis, Ore.	Cirsium lanceolatum

*The writer is indebted to Louise M. Russell for identification of the species marked with an asterisk and to Dr. Knud G. Swenson for identification of the other species listed.

Identification of Viruses

Three strains of cucumber mosaic virus were obtained for use in the transmission tests to be carried out.

The first of these strains was obtained from Dr. J.A. Milbrath of the Department of Botany and Plant Pathology at Oregon State College who, with Dr. Roy A. Young of the same department, isolated it from a diseased daphne plant, Daphne odora Thunberg, and determined that it was a strain of cucumber mosaic virus (61). This virus was acquired from the daphne plant on April 4, 1954, and was maintained through mechanical inoculations* to cucumber and Kentucky 56 tobacco plants, Nicotiana tabacum Linn. var., and in dehydrated local lesions from one of the tobacco plants, until inoculated to young cucumber plants for use in transmission tests, which were begun in June, 1957. This strain will subsequently be referred to as "D-17".

The second strain was also provided by Dr. Milbrath who had received it on December 27, 1954, from the American Type Culture collection of viruses where it was designated "Cucumber Mosaic Common Type Culture #10". This virus was retained through mechanical inoculations to cucumber and Necrotic Turk tobacco plants, Nicotiana

*Inoculations of plants with viruses by means other than by aphids are in this paper considered mechanical inoculations.

tabacum x N. glutinosa Linn. hybrid, and in dehydrated lesions from one of the tobacco plants, until inoculated to young cucumber plants for use in tests. This strain will be referred to as "CMV type".

The third strain was acquired from a virus-diseased gladiolus plant and inoculated to a young cucumber plant by aphids of the species Myzus persicae (Sulzer) on February 27, 1957. The procedure whereby this was accomplished is recounted in the appendix. This virus, which caused the development of cucumber mosaic symptoms in cucumber plants, was maintained through inoculations by Myzus persicae aphids to cucumber plants. This strain of the virus will be referred to as "G-23".

Cucumber mosaic virus (usually) does not infect Bountiful bean plants, Phaseolus vulgaris Linn. var., and occasionally causes local lesions on broadbean plants, in which it seldom becomes systemic (61, p. 282). The virus infects and becomes systemic in Necrotic Turk tobacco plants.

The G-23 and CMV type viruses, in expressed juice from the youngest leaves of infected cucumber plants, were each inoculated by a method similar to that described by Rawlins and Tompkins (74, p. 579) to leaves of Bountiful bean, broadbean and Necrotic Turk tobacco plants. The results of these inoculations were similar for both viruses. The viruses did not infect the Bountiful

bean plants or become systemic in the broadbean plants. However, they caused the appearance of local lesions on the inoculated leaves of the broadbean plants and infected and became systemic in the tobacco plants.

The writer concluded that the gladiolus virus was a strain of cucumber mosaic virus because it is unlikely that any other virus, transmitted by aphids as this virus was, would cause the reactions described when inoculated to cucumber, Bountiful bean, broadbean and Necrotic Turk tobacco plants.

Aphid Transmission Testing Procedure

Cucumber mosaic virus is considered "non-persistent" in respect to the manner of its transmission by insects (100, p. 544). Aphid vectors of this virus can acquire it almost immediately after they begin to feed on an infected plant. If these aphids are starved for a time before they feed on such a plant, the probability that they will transmit the virus to healthy plants on which they subsequently feed is increased.

In the transmission tests here described, virus-infected plants are termed "virus source plants" and healthy plants to which aphids from virus source plants are transferred are termed "test plants".

All of the plants used in these tests were cucumber plants, Cucumis sativus Linn., variety A and C. These plants were grown in soil in six-inch pots or number 10 cans on benches in a greenhouse.

The tests were carried out in a headhouse adjacent to, but separated from, the greenhouse in which aphids and plants were kept.

At the start of each test, approximately 75 apterous aphids were transferred, on the moistened tip of a small brush, into a 50 ml Erlenmeyer flask. In all succeeding cases, when aphids were moved, they were similarly brush-transferred. When the aphids had starved in the flask for at least one-half hour, 15 of them were placed on the

youngest leaves of a virus source plant. After the aphids had been on the source plant for five minutes, 10 of them were transferred to a young test plant. Aphids were transferred from the flask to the source plant and from the source plant to test plants, as described, until 50 of them had been placed on five test plants, 10 aphids per plant.

For each five test plants used, 10 additional aphids were transferred directly from the aphid collection being used to each of two healthy cucumber plants identical with, and grown in the same lot with, those used as test plants. This was done, as a check, so an indication could be obtained of whether the aphids were transmitting viruses to test plants from plants on which they fed before the test was started.

When aphids had remained on the test or check plants on which they were placed for one hour or more, these plants, and the virus source plant used, were fumigated with nicotine for five minutes to kill the aphids on them and were placed on benches in the greenhouse.

At the completion of each test, five additional healthy cucumber plants, identical with and grown in the same lot with those used as test plants, and which were never removed from the greenhouse, were placed on the same bench with the plants to which aphids had been transferred. This was done so any transmission of viruses by stray

aphids in the greenhouse might be indicated.

Tests, as described above, were carried out at least twice with every aphid-virus combination used. More than two tests, with a maximum of six, were made with any such combination with which transmission was not achieved in two tests.

Since differences could often be observed in the feeding behavior of aphids on different days, each of the tests using any particular aphid-virus combination was made on a different day. Also, any single day's testing never involved the use of aphids from more than one collection, thereby reducing the chances of accidental mixing of aphids from different collections.

The greenhouse units in which plants used in tests were kept were fumigated with nicotine or TEPP (Tetraethyl Pyrophosphate) whenever insects were noticed therein.

RESULTS

Transmission of CMV Type and G-23

The results of tests to determine the ability of each of the species of aphids tested to transmit the G-23 and CMV type strains of cucumber mosaic virus are given in table 2. This table shows that 11 of the 13 species tested transmitted at least one of the two strains and nine of these 11 species transmitted both strains.

The species Macrosiphum solanifolii (Ashm.), Myzus persicae Sulzer, Macrosiphum pisi (Kalt.), Amphorophora sonchi (Oest.), Amphorophora rhododendri (Wilson), Macrosiphum rosae (Linn.) and Aphis cardui Linn. readily transmitted both strains of the virus. Aphis fabae Scop., Rhopalosiphum fitchii (Sand.), Brevicoryne brassicae (Linn.) and Macrosiphum barri Essig transmitted both strains at a low rate or transmitted only one of the strains, and Macrosiphum dirhodum (Walker) and Macrosiphum granarium (Kirby) failed to transmit either of the two strains.

Aphids of the species Macrosiphum barri were tested only twice with each of the two strains, even though they did not transmit the CMV type strain. These aphids were not tested further because it was very difficult to collect enough of them for more tests.

Aphids of the two species which failed to transmit either of the two strains, Macrosiphum granarium and Macrosiphum dirhodum, were very active when placed on cucumber plants and few of them fed on these plants. Because of this, tests with these aphids were discontinued after aphids of both species had been tested four times with both strains.

All of the check plants used remained uninfected by viruses.

Considering all tests, strains of cucumber mosaic virus were transmitted to 157 of 680 test plants, or to slightly more than 23 per cent of the test plants. The G-23 strain was transmitted to 79 test plants and the CMV type strain to 78 test plants.

TABLE 2

RESULTS OF ATTEMPTS TO TRANSMIT G-23 AND CMV TYPE

WITH DIFFERENT SPECIES OF APHIDS

Collection Number	Species	Virus Strain	Number of Tests	Number of Aphids Used (10 per Plant)	Number of Infections*
1	*Aphis fabae* Scop.	CMV type	4	200	3/20
		G-23	4	200	0/20
2	*Aphis fabae* Scop.	CMV type	4	200	0/20
		G-23	4	200	0/20
3	*Aphis fabae* Scop.	CMV type	2	100	2/10
		G-23	2	100	3/10
4	*Aphis fabae* Scop.	CMV type	4	200	0/20
		G-23	4	200	0/20
5	*Aphis fabae* Scop.	CMV type	4	200	0/20
		G-23	4	200	0/20
6	*Aphis fabae* Scop.	CMV type	4	200	2/20
		G-23	4	200	1/20
7	*Macrosiphum solanifolii* (Ashm.)	CMV type	2	100	5/10
		G-23	2	100	5/10
8	*Macrosiphum solanifolii* (Ashm.)	CMV type	2	100	1/10
		G-23	2	100	8/10

TABLE 2 Cont'd

Collection Number	Species	Virus Strain	Number of Tests	Number of Aphids Used (10 per Plant)	Number of Infections*
9	Macrosiphum solanifolii (Ashm.)	CMV type	2	100	1/10
		G-23	2	100	5/10
10	Macrosiphum solanifolii (Ashm.)	CMV type	2	100	9/10
		G-23	2	100	3/10
11	Macrosiphum solanifolii (Ashm.)	CMV type	2	100	4/10
		G-23	2	100	8/10
12	Macrosiphum solanifolii (Ashm.)	CMV type	2	100	8/10
		G-23	2	100	2/10
13	Macrosiphum solanifolii (Ashm.)	CMV type	2	100	2/10
		G-23	2	100	1/10
14	Rhopalosiphum fitchii (Sand.)	CMV type	6	300	1/30
		G-23	6	300	0/30
15	Macrosiphum granarium (Kirby)	CMV type	4	200	0/20
		G-23	4	200	0/20
16	Macrosiphum dirhodum (Walk.)	CMV type	4	200	0/20
		G-23	4	200	0/20
17	Brevicoryne brassicae (Linn.)	CMV type	4	200	1/20
		G-23	4	200	5/20
18	Myzus persicae (Sulz.)	CMV type	2	100	3/10
		G-23	2	100	4/10

TABLE 2 Cont'd

Collection Number	Species	Virus Strain	Number of Tests	Number of Aphids Used (10 per Plant)	Number of Infections*
19	Macrosiphum pisi (Kalt.)	CMV type	2	100	7/10
		G-23	2	100	4/10
20	Amphorophora sonchi (Oest.)	CMV type	2	100	9/10
		G-23	2	100	6/10
21	Amphorophora rhododendri (Wils.)	CMV type	2	100	4/10
		G-23	2	100	8/10
22	Macrosiphum rosae (Linn.)	CMV type	2	100	9/10
		G-23	2	100	9/10
23	Macrosiphum barri Essig	CMV type	2	100	0/10
		G-23	2	100	3/10
24	Aphis cardui (Linn.)	CMV type	2	100	7/10
		G-23	2	100	4/10

*Numerator = Number of Infections; Denominator = Number of Test Plants

Transmission of CMV Type by Different Collections of Aphis fabae Scopoli

From the results of tests of different collections of aphids of the species Aphis fabae Scop., it appeared as though some collections of this species might be unable to transmit the strains of cucumber mosaic virus used. To investigate this possibility, further tests were made to determine whether aphids from a collection of this species which had not been shown to contain vectors of either of the virus strains used (collection #2) could transmit the CMV type strain. Also, as a check and for comparison, aphids from a collection of the same species which had been shown to contain vectors of both strains of the virus (collection #3) were similarly tested. The testing procedure used was the same as that previously described. Aphids from both collections were tested on each of five days and the order in which the collections were used in tests on each day was randomly determined. The results of these tests, which are given in table 3, show that aphids from both collections tested were able to transmit CMV type. None of the check plants used in these tests became infected with viruses.

RESULTS OF TESTS TO DETERMINE THE ABILITY OF APHIDS FROM EACH OF TWO COLLECTIONS OF *APHIS FABAE* SCOPOLI TO TRANSMIT CMV TYPE

Test Date	Collection Number (In Order Tested)	Number of Aphids Used (10 per Plant)	Number of Infections*
26 Sep 57	2	50	0/5
	3	50	0/5
27 Sep 57	3	50	1/5
	2	50	1/5
17 Oct 57	3	50	2/5
	2	50	0/5
28 Oct 57	2	50	0/5
	3	50	0/5
30 Oct 57	3	50	0/5
	2	50	0/5

*Numerator = Number of Infections
Denominator = Number of Test Plants

Nontransmission of D-17

As previously indicated, all of the strains of cucumber mosaic virus to be used in transmission tests were inoculated to healthy cucumber plants shortly before the transmission tests were to begin. The D-17 and CMV type strains were mechanically inoculated to these plants whereas the plants inoculated with the G-23 strain were inoculated by aphids of the species Myzus persicae (Sulzer).

Cucumber mosaic virus is commonly inoculated to healthy plants by aphids under field conditions. It was therefore thought desirable to inoculate the D-17 and CMV type strains of the virus to healthy cucumber plants with Myzus persicae aphids and to use the resulting aphid-inoculated plants, and the plants inoculated with G-23 by aphids, as virus source plants in the transmission tests to be made.

When attempts were made to do this, the CMV type strain was readily transmitted to healthy cucumber plants. The D-17 strain, however, could not be transmitted to healthy cucumber plants, although approximately 600 aphids were used in repeated attempts to transmit this strain.

The inability of Myzus persicae aphids to transmit the D-17 virus was unexpected since Dr. Knud G. Swenson of the Department of Entomology at Oregon State College, in unpublished work carried out in the fall of 1956, was

able to transmit the D-17 strain from infected to healthy cucumber plants with the aphid species Macrosiphum rosae (Linn.), Macrosiphum solanifolii (Ashm.), Amphorophora rubitoxica Knowlton, Macrosiphum pisi (Kalt.), Aphis gossypii Glover and Amphorophora sonchi (Oest.).* He was unable to transmit the virus with Aphis fabae Scop., Brevicoryne brassicae (Linn.), Hyalopterus atriplicis (Linn.), Aphis helianthi Monell, Macrosiphum granarium (Kirby) or Anuraphis tulipae Boyer de Fonscolombe.

*The writer is indebted to Dr. Swenson for the information concerning aphid transmission of D-17 here presented.

Comparison of Transmissibility of CMV Type and D-17 by Myzus persicae (Sulzer)

To inquire into this nontransmission of D-17, a series of tests were made to compare the transmissibility of D-17 and CMV type by aphids of the species Myzus persicae (Sulzer). The testing procedure previously described was followed in these tests. Both of the viruses were tested for transmissibility on each of 10 days and the order in which they were used in tests on each day was randomly determined. The results of these tests are given in table 4. They show that Myzus persicae aphids transmitted the CMV type strain, but not the D-17 strain, of cucumber mosaic virus. None of the check plants used became infected with viruses.

Since the D-17 strain could not be transmitted by Myzus persicae aphids, it was not used, as were the G-23 and CMV type strains, in transmission tests with different species of aphids.

TABLE 4

COMPARISON OF TRANSMISSIBILITY OF CMV TYPE AND D-17 BY MYZUS PERSICAE (SULZER) APHIDS

Test Date	Virus Strain (In Order Tested)	Number of Aphids Used (10 per Plant)	Number of Infections*
28 Aug 57	D-17	50	0/5
	CMV type	50	1/5
1 Oct 57	D-17	50	0/5
	CMV type	50	1/5
2 Oct 57	D-17	50	0/5
	CMV type	50	0/5
18 Oct 57	CMV type	50	1/5
	D-17	50	0/5
19 Oct 57	CMV type	50	4/5
	D-17	50	0/5
21 Oct 57	D-17	50	0/5
	CMV type	50	1/5
22 Oct 57	D-17	50	0/5
	CMV type	50	0/5
23 Oct 57	CMV type	50	2/5
	D-17	50	0/5
17 Jan 58	CMV type	50	0/5
	D-17	50	0/5
18 Jan 58	CMV type	50	0/5
	D-17	50	0/5

TOTAL INFECTIONS OBTAINED

D-17 - 0/50
CMV type - 10/50

*Numerator = Number of Infections
Denominator = Number of Test Plants

DISCUSSION

The results of the transmission tests carried out and the many reports reviewed of aphid transmission of strains, or possible strains, of cucumber mosaic virus both indicate that the virus is likely to be transmitted by many species of aphids. It follows that nearly all species of aphids which feed on gladiolus plants may be concerned with the spread of the white break disease. This conclusion is supported by the fact that 10 of the 13 species of aphids tested transmitted the strain of cucumber mosaic virus acquired from a virus-diseased gladiolus plant.

During the investigations reported, special efforts were made to collect and test aphids found colonizing on gladiolus plants. With the exception of black bean aphids, Aphis fabae Scopoli, few such aphids were observed. Those aphids, other than black bean aphids, which were found colonizing on gladiolus plants were collected, colonized in the greenhouse, and tested, as previously described. All of these aphids were later identified as potato aphids, Macrosiphum solanifolii (Ashmead). Aphids of this species are good vectors of cucumber mosaic virus and, since they occasionally colonize on gladiolus plants, appear to be important in respect to spread of the white break disease of gladiolus.

As indicated, Aphis fabae aphids are commonly found colonizing on gladiolus plants. In addition, these aphids can often be observed on gladiolus plants throughout the summer. Aphis fabae has frequently been reported as a vector of strains of cucumber mosaic virus (84, p. 217) (81, p. 586) (83, p. 529) (78, p. 553) (59, p. 51) (91, p. 115) (69, p. 59) (82, p. 286) (62, p. 762) (35, p. 67) (106, p. 451) (38, p. 84). However, this species has also been reported as a non-vector of cucumber mosaic virus in lilies (13, p. 530) and of the chrysanthemum aspermy strain of the virus (8, p. 322-323) and Swenson, in work previously described, was unable to transmit the daphne strain of the virus with this species. In addition, Simons (84, p. 217) and Severin (78, p. 553) indicated that Aphis fabae was not as efficient a vector of strains of cucumber mosaic virus as were other species of aphids with which they worked.

Since Aphis fabae aphids are commonly found on gladiolus plants and because of the contrasting reports concerning the ability of these aphids to transmit cucumber mosaic virus, it was desirable to thoroughly test this species for its ability to transmit strains of cucumber mosaic virus. Aphids from six different collections of this species were consequently tested in the transmission tests described. The results of these tests indicate that aphids of the species Aphis fabae can transmit

strains of cucumber mosaic virus, but that they are not as efficient in this respect as are most of the other aphid species tested. Nevertheless, aphids of this species are probably important in the spread of the white break disease because of their abundance in gladiolus fields.

That many species of aphids may be able to act as vectors of cucumber mosaic virus and the fact that the virus infects a wide variety of plants, some of which are very common, should be considered when methods to reduce the spread of diseases caused by this virus are being determined. An additional factor to be considered is that this virus can be quickly acquired from, and inoculated to, plants by its aphid vectors. This is important because insecticides which can kill aphids rapidly enough to prevent them from transmitting the virus are not yet available. Observations indicate that migrating aphids, which are apt to feed on each of many plants for short periods of time, may be largely responsible for carrying cucumber mosaic virus to and within gladiolus fields. In view of the preceding considerations, the task of effectively reducing aphid spread of the white break disease seems very difficult.

The inability of Myzus persicae (Sulzer) to transmit the daphne strain of cucumber mosaic virus suggests that this virus, which at one time could be transmitted by aphids, may have lost its insect transmissibility.

Reports of the loss of insect transmissibility by viruses have previously been made. In any event, the daphne strain of cucumber mosaic virus was not transmitted by Myzus persicae under conditions in which this species was able to transmit the type strain of the virus.

SUMMARY

A disease of the gladiolus in Oregon, known as white break of gladiolus, is commonly caused by cucumber mosaic virus. In seeking information concerning the spread of this disease, it was desirable to determine whether cucumber mosaic virus is likely to be transmitted by few or many species of aphids. Investigations were carried out to obtain this information.

Reports concerning insect transmission of cucumber mosaic virus were extensively reviewed.

Tests were made to determine the ability of each of 13 species of aphids to transmit strains of the virus. The results of these tests show that the type strain of cucumber mosaic virus and/or a strain of the virus acquired from a gladiolus plant were transmitted by 11 of the 13 species of aphids tested. These strains were readily transmitted by aphids of the species Macrosiphum solanifolii (Ashmead), Myzus persicae (Sulzer), Macrosiphum pisi (Kaltenbach), Amphorophora sonchi (Oestlund), Amphorophora rhododendri (Wilson), Macrosiphum rosae (Linnaeus) and Aphis cardui Linn. Aphids of the species Aphis fabae Scopoli, Rhopalosiphum fitchii (Sanderson), Brevicoryne brassicae (Linn.) and Macrosiphum barri Essig transmitted both strains at a low rate or transmitted only one of the strains, and those of the species

Macrosiphum dirhodum (Walker) and Macrosiphum granarium (Kirby) failed to transmit either of the two strains.

Repeated attempts to transmit, by Myzus persicae aphids, a strain of cucumber mosaic virus isolated from a daphne plant were unsuccessful. The results of tests made to further investigate this nontransmission show that the daphne virus, which had previously been transmitted by aphids, could not be transmitted by Myzus persicae aphids under conditions in which these aphids transmitted the type strain of cucumber mosaic virus.

The results of the transmission tests and the reports of insect transmission of cucumber mosaic virus reviewed indicate that the virus can be transmitted by many species of aphids. It follows that many species of aphids may be involved in the spread of the white break disease of gladiolus. Macrosiphum solanifolii and Aphis fabae aphids appear to be particularly important in this respect.

A review of reports of the occurrence of cucumber mosaic virus in the gladiolus, an account of the procedure whereby viruses were isolated from gladiolus plants by Myzus persicae aphids, and a referenced list of aphid species reported as vectors of strains, or possible strains, of cucumber mosaic virus are given in the appendix.

BIBLIOGRAPHY

1. Adlerz, Warren Clifford. Factors affecting aphid transmission of bean yellow mosaic virus. Ph.D. thesis. Corvallis, Oregon State College, 1958. 40 numb. leaves.

2. Allard, H. A. Further studies of the mosaic disease of tobacco. Journal of Agricultural Research 10:615-632. 1917.

3. Allard, H. A. The mosaic disease of tobacco. 1914. 33 p. (U. S. Department of Agriculture. Bulletin No. 40).

4. Behr, L. Die Gelbfleckigkeit des Spinates (Spinacia oleracea L.) Untersuchungen über einen mitteldeutschen Virustamm. Archiv für die gesamte Virusforschung 6:1-28. 1955. (Abstracted in Review of Applied Mycology 34:426. 1955.)

5. Berkeley, G. H. Gladiolus viruses. (Abstract) Phytopathology 41:3-4. 1951.

6. Berkeley, G. H. Some viruses affecting gladiolus. Phytopathology 43:111-115. 1953.

7. Bhargava, K. S. Some properties of four strains of cucumber mosaic virus. Annals of Applied Biology 38:377-388. 1951.

8. Blencowe, J. W. and John Caldwell. Aspermy - a new virus disease of the tomato. Annals of Applied Biology 36:320-326. 1949.

9. Bridgmon, G. H. Gladiolus as a virus reservoir. (Abstract) Phytopathology 41:5. 1951.

10. Bridgmon, G. H. and J. C. Walker. Gladiolus as a virus reservoir. Phytopathology 42:65-70. 1952.

11. Brierley, Philip. Evidence on the significance of cucumber mosaic and tobacco ringspot viruses in gladiolus. Plant Disease Reporter 36:48-50. 1952.

12. Brierley, Philip and Floyd F. Smith. Carnation and gladiolus virus diseases pose serious problems. Florists' Review 99:31-33. 1947.

13. Brierley, Philip and Floyd F. Smith. Studies on lily virus diseases: The necrotic-fleck complex in Lilium longiflorum. Phytopathology 34:529-555. 1944.

14. Brierley, Philip, Floyd F. Smith, and S. P. Doolittle. Experiments with tomato aspermy virus from chrysanthemum. (Abstract) Phytopathology 43:404. 1953.

15. Carter, Walter. Aphis transmittal of Commelina nudiflora Linnaeus mosaic to pineapple. Annals of the Entomological Society of America 30:155-161. 1937.

16. Celino, Martin S. Experimental transmission of the mosaic of abacá, or Manila hemp plant (Musa textilis Née). Philippine Agriculturist 29:379-403. 1940.

17. Chamberlain, E. E. Cucumber-mosaic (Cucumis Virus 1 of Smith, 1937). New Zealand Journal of Science and Technology, A, 21:74-90. 1939.

18. Chamberlain, E. E. Narrow-leaf - a virus disease of tomatoes. New Zealand Journal of Agriculture 49:257-263. 1934.

19. Chamberlain, E. E. Virus diseases of tree tomato (Cyphomandra betacea Sendt.) 1. Cucumber-mosaic (Cucumis virus 1 of Smith, 1937). New Zealand Journal of Science and Technology, A, 29:256-260. 1948.

20. Dickson, R. C. A working list of the names of aphid vectors. Plant Disease Reporter 39:445-452. 1955.

21. Doncaster, J. P. and B. Kassanis. The shallot aphis, Myzus ascalonicus Doncaster, and its behavior as a vector of plant viruses. Annals of Applied Biology 33:66-68. 1946.

22. Doolittle, S. P. A new infectious disease of cucumber. Phytopathology 6:145-147. 1916.

23. Doolittle, S. P. Commelina nudiflora, a monocotyledonous host of celery mosaic. (Abstract) Phytopathology 21:114-115. 1931.

24. Doolittle, S. P. The mosaic disease of cucurbits. 1920. 69 p. (U. S. Department of Agriculture. Bulletin no. 879).

25. Doolittle, S. P. and F. L. Wellman. Commelina nudiflora, a monocotyledonous host of a celery mosaic in Florida. Phytopathology 24:48-61. 1934.

26. Doolittle, S. P. and M. N. Walker. Aphis transmission of cucumber mosaic. (Abstract) Phytopathology 18:143. 1928.

27. Doolittle, S. P. and M. N. Walker. Further studies on the overwintering and dissemination of cucurbit mosaic. Journal of Agricultural Research 31:1-58. 1925.

28. Doolittle, S. P. and M. N. Walker. Notes on cucurbit mosaic. (Abstract) Phytopathology 12:42-43. 1922.

29. Elmer, O. H. Transmissibility and pathological effects of the mosaic disease. 1925. p. 40-91. (Iowa. Agricultural Experiment Station. Research Bulletin no. 82).

30. Faan, H. C. and J. Johnson. The overwintering of the cucumber mosaic virus. Phytopathology 41:1001-1010. 1951.

31. Freitag, Julius H. A comparison of the transmission of four cucurbit viruses by cucumber beetles and by aphids. (Abstract) Phytopathology 31:8. 1941.

32. Freitag, Julius H. Beetle transmission, host range, and properties of squash mosaic virus. Phytopathology 46:73-81. 1956.

33. Fry, P. R. Two virus diseases of gladiolus. New Zealand Journal of Science and Technology, ser A, 34:460-464. 1953.

34. Gigante, R. Il mosaico del Sedano. Rome. Stazione di Patologia vegetale. Bollettino N. S. 16:99-114. 1936. (Abstracted in Review of Applied Mycology 16:227-228. 1937).

35. Govier, D. A. The properties of tomato aspermy virus and its relationship with cucumber mosaic virus. Annals of Applied Biology 45:62-73. 1957.

36. Harter, L. L. Mosaic of lima beans Phaseolus lunatus macrocarpus. Journal of Agricultural Research 56:895-906. 1938.

37. Heinze, Kurt. Die Überträger pflanzlicher Viruskrankheiten. Mitteilungen aus der Biologischen Zentralanstalt für Land-und Forstwirtschaft (Berlin) 71:1-127. 1951.

38. Heinze, Kurt. Übertragung und Überwinterung des Lupinbräune - Virus. Mitteilungen aus der Biologischen Reichsanstalt für Land-und Forstwirtschaft. (Berlin) 59:84-86. 1939.

39. Heinze, Kurt. Virusübertragungsversuche mit Blattläusen auf Dahlien, Gurken, Zwiebeln, Wasserrüben und einigen anderen Pflanzen. Zeitschrift für Pflanzenkrankheiten, Pflanzenpathologie und Pflanzenschutz. 59:3-13. 1952.

40. Heinze, Kurt. Weitere Versuche zur Übertrangung von phytopathogenen Viren mit Blattläusen. Nachrichtenblatt des Deutschen Pflanzenschutzdienstes. (Braunschweig) 9:22-25. 1957.

41. Heinze, Kurt. Zur Übertragung pflanzlicher Viruskrankheiten durch Blattläuse. Nachrichtenblatt des Deutschen Pflanzenschutzdienstes (Braunschweig) 2:49-53. 1950.

42. Hoggan, Ismé A. Further studies on aphid transmission of plant viruses. Phytopathology 21:199-212. 1931.

43. Hoggan, Ismé A. Some viruses affecting spinach and certain aspects of insect transmission. Phytopathology 23:446-474. 1933.

44. Hoggan, Ismé A. Studies on aphid transmission of plant viruses. Journal of Bacteriology 19:21-22. 1930.

45. Hoggan, Ismé A. The peach aphid (Myzus persicae Sulz.) as an agent in virus transmission. Phytopathology 19:109-123. 1929.

46. Hoggan, Ismé A. Transmission of cucumber mosaic to spinach. Phytopathology 20:103-105. 1930.

47. Hollings, M. Investigation of chrysanthemum viruses 1. Aspermy flower distortion. Annals of Applied Biology 43:86-102. 1955.

48. Hopkins, J. C. F. Annual report of the branch of plant pathology for the year ending 31st December, 1940. Salisbury, Office of the Senior Plant Pathologist, Department of Agriculture (Southern Rhodesia). 1941. 8 p. (Abstracted in Review of Applied Mycology 20:448-449. 1941.)

49. Jagger, I. C. Experiments with the cucumber mosaic disease. Phytopathology 6:148-151. 1916.

50. Jones, Leon K. and Grover Burnett. Virous diseases of greenhouse-grown tomatoes. Pullman, 1935. 36 p. (Washington. Agricultural Experiment Station. Bulletin no. 308).

51. Kassanis, B. Studies on dandelion yellow mosaic and other virus diseases of lettuce. Annals of Applied Biology 34:420. 1947.

52. Kent, G. C. Abacá mosaic. Philippine Agriculturist 37:555-577. 1954.

53. Klinkowski, M. Beiträge zur Kenntnis der Virosen der Gladiole in Mitteldeutschland. Mitteilungen aus der Biologischen Bundesanstalt für Land-und Forstwirtschaft (Berlin) 85:139-150. 1956.

54. Kristensen, H. R. Virussygdome hos Agurker i Danmark. Horticultura 10:161-172. 1956. (English summary). (Abstracted in Review of Applied Mycology 36:165. 1957.)

55. Magee, C. J. P. A new virus disease of bananas. Agricultural Gazette of New South Wales 41:929. 1930.

56. Magee, C. J. P. Transmission of infectious chlorosis or heart-rot of the banana and its relationship to cucumber mosaic. Journal of the Australian Institute of Agricultural Science 6:44-47. 1940. (Abstracted in Review of Applied Mycology 19:481-482. 1940.)

57. Magee, C. J. P. Woodiness or mosaic disease of passion fruit. Agricultural Gazette of New South Wales 59:199-202. 1948.

58. McLean, D. M. Studies on mosaic of cowpeas, Vigna sinensis. Phytopathology 31:420-430. 1941.

59. McClintock, J. A. and Loren B. Smith. True nature of spinach-blight and relation of insects to its transmission. Journal of Agricultural Research 14:1-60. 1918.

60. McWhorter, Frank P. A localized occurrence of cucumber mosaic virus in gladiolus. Plant Disease Reporter 41:141-142. 1957.

61. Milbrath, J. A. and Roy A. Young. Cucumber mosaic virus and alfalfa mosaic virus isolated from Daphne odora. Plant Disease Reporter 40:279-283. 1956.

62. Mischke, W. Einige durch Insekten übertragbare Viruskrankheiten an Topfpflanzen, Pflanzenschutz 9:96-97. 1957. (Abstracted in Review of Applied Mycology 36:762. 1957.)

63. Mogendorff, N. "Fern-leaf" of tomato. Phytopathology 20:25-46. 1930.

64. New Zealand, Department of Scientific and Industrial Research. Twenty-fifth annual report - 1951. R. E. Owen, Government printer. 1951. 80 p.

65. Nienow, Inez. The identification and characterization of a virus causing mosaic in Mertensia virginica. Phytopathology 38:62-69. 1948.

66. Noble, R. J. and N. S. Noble. Aphid vectors of the virus of woodiness or bullet disease in passion fruit (Passiflora edulis Sims). Journal of the Royal Society of New South Wales 72:293-317. 1939.

67. Noble, R. J. and N. S. Noble. The woodiness disease of passion fruit. Aphid carriers demonstrated. Agricultural Gazette of New South Wales 50:19-21. 1939.

68. Ogilvie, Lawrence L. and Carl E. F. Guterman. A mosaic disease of the Easter lily. Phytopathology 19:311-316. 1929.

69. Parris, G. K. The diseases of truck crops in Hawaii. Honolulu, 1938. 78 p. (University of Hawaii. Extension Service Bulletin no. 33).

70. Poole, R. F. Celery mosaic. Phytopathology 12:151-154. 1922.

71. Price, W. C. Classification of lily-mosaic virus. Phytopathology 27:561-569. 1937.

72. Price, W. C. Comparative host ranges of six plant viruses. American Journal of Botany 27:530-541. 1940.

73. Price, W. C. Isolation and study of some yellow strains of cucumber mosaic virus. Phytopathology 24:743-761. 1934.

74. Rawlins, T. E. and C. M. Tompkins. Studies on the effect of carborundum as an abrasive in plant virus inoculations. Phytopathology 26:578-587. 1936.

75. Roland, G. Étude d'une mosaïque observée sur Apium graveolens. Parasitica 7:63-68. 1951. (Flemmish summary). (Abstracted in Review of Applied Mycology 31:269. 1952.)

76. Semal, J. Données nouvelles sur la transmission des virus de la Betterave par Myzus ascalonicus Doncaster. Parasitica 13:1-12. 1957. (English summary). (Abstracted in Review of Applied Mycology 36:628. 1957.)

77. Semal, J. Transmission par pucerons de Cucumis Virus 1 var. Chr. Noordam de Céleri à Céleri. Parasitica 12:71-73. 1956. (English summary). (Abstracted in Review of Applied Mycology 36:446. 1957.)

78. Severin, Henry H. P. Additional virus diseases of spinach in California. Hilgardia 18:553-566. 1948.

79. Severin, Henry H. P. Celery calico on perennial delphiniums and certain other host plants. Hilgardia 14:441-464. 1942.

80. Severin, Henry H. P. Multiple viruses of tomato inducing malformation and leaf symptoms. Hilgardia 20:109-136. 1950.

81. Severin, Henry H. P. Viruses that induce breaking in color of flower petals in pansies and violas. Hilgardia 17:577-594. 1947.

82. Severin, Henry H. P. and C. M. Tompkins. Aphid transmission of a mosaic virus and symptoms of other virus diseases of Primula obconica. Hilgardia 20: 279-298. 1950.

83. Severin, Henry H. P. and Julius H. Freitag. Outbreak of western cucumber mosaic on sugar beets. Hilgardia 18:523-530. 1948.

84. Simons, John N. Some plant-vector-virus relationships of southern cucumber mosaic virus. Phytopathology 45:217-219. 1955.

85. Simons, John N. Three strains of cucumber mosaic virus affecting bell pepper in the Everglades area of South Florida. Phytopathology 47:145-150. 1957.

86. Smith, Floyd F. and Philip Brierley. Aphid transmission of lily viruses during storage of the bulbs. Phytopathology 38:841-844. 1948.

87. Smith, Floyd F. and Philip Brierley. Insect transmission of plant viruses. Annual Review of Entomology 1:299-322. 1956.

88. Smith, Floyd F. and Philip Brierley. Preliminary report on some mosaic diseases of iridaceous plants. Phytopathology 34:593-598. 1944.

89. Smith Floyd F. and Philip Brierley. Simulation of lily rosette symptoms by feeding injury of the foxglove aphid. Phytopathology 38:849-851. 1948.

90. Smith, Kenneth M. A virus disease of Primula obconica and related plants. Annals of Applied Biology 22: 236-238. 1935.

91. Smith, Kenneth M. Recent advances in the study of plant viruses. Philadelphia, Blakiston, 1934. 423 p.

92. Smith, Kenneth M. Textbook of plant virus diseases. London, Churchill, 1957. 652 p.

93. Smith, Kenneth M. Viruses and virus diseases. Journal of the Royal Horticultural Society 74:521-528. 1949.

94. Snow, G. F. Ringspot and bean mosaic viruses from gladiolus. Ph.D. thesis. Corvallis, Oregon State College, 1956. 78 numb. leaves.

95. Tompkins, C. M. and John T. Middleton. A mosaic disease of Primula obconica and its control. Journal of Agricultural Research 63:671-679. 1941.

96. Van Koot, Y. and (Miss J.) Camfferman. Een ziekte bij Tomaat, veroorzaakt door een combinatie van Tomaten-en Komkommermozaeik (Nicotiana-virus 1 + Cucumis-virus 1). Tijdschrift over PlantenZiekten, 58:14-20, 1952.

97. Wade, G. C. Gladiolus diseases. Tasmanian Journal of Agriculture 19:36-40. 1948.

98. Walker, M. N. The relation of certain species of Physalis to the overwintering of the mosaic disease of cucumber. Phytopathology 15:733-744. 1925.

99. Watson, Marion A. Aphis transmission of some plant viruses. Proceedings of the Royal Society of London, ser. B, 125:305-307. 1938.

100. Watson, Marion A. and Florence M. Roberts. A comparative study of the transmission of Hyoscyamus virus 3, potato virus Y and cucumber virus 1 by the vectors Myzus persicae (Sulz.), M. circumflexus (Buckton), and Macrosiphum gei (Koch.). Proceedings of the Royal Society of London, ser B, 127:543-576. 1939.

101. Wellman, F. L. A disease of banana, markedly similar to bunchy top, produced by celery virus 1 in U. S. A. Phytopathology 24:1032-1034. 1934.

102. Wellman, F. L. Identification of celery virus 1, the cause of southern celery mosaic. Phytopathology 24:695-725. 1934.

103. Wellman, F. L. Infection of Zea mays and various other Gramineae by the celery virus in Florida. Phytopathology 24:1035-1037. 1934.

104. Wellman, F. L. The host range of the southern celery-mosaic virus. Phytopathology 25:377-404. 1935.

105. Whipple, O. C. and J. C. Walker. Strains of cucumber mosaic virus pathogenic on bean and pea. Journal of Agricultural Research 62:27-60. 1941.

106. Yu, T. F. A mosaic disease of cowpea (Vigna sinensis Endl.). Annals of Applied Biology 33:450-454. 1946.

APPENDIX

APPENDIX

Occurrence of Cucumber Mosaic Virus in Gladiolus Plants

Smith and Brierley (88, p. 597) reported the occurrence of cucumber mosaic virus in Sparaxis in 1944 and believed that their report constituted the first record of infection of a plant in the family Iridaceae with this virus.

In 1948 Wade (97, p. 39) stated that N. H. White had found that a mosaic of gladiolus in Tasmania, characterized by pale-green mottling of foliage and breaking of flower color, was caused by cucumber mosaic virus and Smith (93, p. 523), the following year, indicated that this virus was the cause of color breaks in gladiolus blossoms in England.

Apparently the first reports of cucumber mosaic virus in gladiolus in North America were by Berkeley (5, p. 3-4) and Bridgmon (9, p. 5) who both isolated the virus from this plant in 1951. Bridgmon acquired the virus, and other viruses, from plants showing a leaf mottle and flower break but established no relationship between these symptoms and cucumber mosaic virus.

The gladiolus has since been reported as a host of cucumber mosaic virus numerous times (30, p. 1005) (64, p. 55) (10, p. 69) (11, p. 50) (6, p. 111) (33, p. 463) (54, p. 165) (53) (94, p. 2) (60, p. 141). Most of

these reports implicate this virus as the cause, or partial cause, of a variety of foliage symptoms and blossom discolorations often observed in the gladiolus.

Snow (94, p. 2), as quoted in the introduction, related in 1956 that the symptoms associated with white break of gladiolus in Oregon are at least partially caused by cucumber mosaic virus. McWhorter (60, p. 141), the following year, indicated that a white break of gladiolus in Oregon is caused by strains of cucumber mosaic virus. He stated that "the disease is easily noted in colored varieties because of contrasty white blotching of flowers accompanied by crinkling, shrinking, and other flower deformations, and because of chlorotic streaking and blotching of the foliage."

A white break of gladiolus occuring in the Eastern United States (12, p. 31-32) is apparently not the same as that present in Oregon.

Isolation of Viruses from Gladiolus Plants by Myzus persicae (Sulzer)

Twenty-six corms of the gladiolus variety Friendship, taken from a field in which the gladiolus crop was heavily damaged by white break, were planted in the greenhouse in January, 1957.

Aphids of the species Myzus persicae (Sulzer) were used in attempts to transmit viruses from each of the shoots which developed from these corms to healthy cucumber and broadbean plants.

In each attempt, aphids were starved as previously described and then were individually placed on the shoot being used. The actual feeding of each of the aphids which fed on the shoot was observed with a hand lens and timed with a stop watch. Five aphids which fed and naturally terminated their feeding within 15 to 60 seconds were transferred to a healthy young cucumber plant. Five additional aphids, which likewise fed, were transferred to a healthy young broadbean plant. The aphids were left on the healthy plants at least one hour before the plants were fumigated and placed in the greenhouse.

Viruses were transmitted in this manner from eight of the 26 gladiolus shoots to cucumber plants, in which they caused cucumber mosaic symptoms to develop, and from 13 of the shoots to broadbean plants, in which they caused

bean yellow mosaic symptoms to develop.

Blossoms eventually developed on only seven of the 26 gladiolus plants grown. All of these blossoms were marked with white streaks or blotches. When attempts were made to transmit viruses from these blossoms, using the procedure described above, viruses were transmitted from the blossoms of four of the seven gladiolus plants to cucumber plants. No viruses were transmitted from the blossoms to broadbean plants.

TABLE 5

REFERENCED LIST OF APHID SPECIES REPORTED AS VECTORS OF STRAINS, OR POSSIBLE STRAINS, OF CUCUMBER MOSAIC VIRUS

Species	Bibliographical References
Amphorophora lactucae (Linnaeus)	41
Amphorophora rhododendri (Wilson)	*
Amphorophora rubitoxica Knowlton	x
Amphorophora sonchi (Oestlund)	x *
Amphorophora viciae (Kaltenbach)	40
Aphis abbreviata Patch	38
Aphis apigraveolens Essig	79, 81
Aphis apii Theobald	79, 81, 82
Aphis armoraciae Cowen	79, 81
Aphis cardui Linn.	*
Aphis cirsii-acanthoidis Scopoli	40
Aphis craccae (Linn.)	41
Aphis fabae Scop.	* 35, 38, 59, 62, 69, 78, 81, 82, 83, 84, 91, 106
Aphis gossypii Glover	x 13, 15, 17, 22, 23, 24, 25, 26, 27, 28, 29, 36, 38, 49, 50, 56, 57, 58, 71, 79, 80, 81, 82, 83, 84, 85, 98, 101, 103, 104, 106

TABLE 5 Cont'd

Species	Bibliographical References
Aphis helichrysi Kalt.	41, 47
Aphis inculta Walker	79, 81, 82
Aphis mordwilkiana Dobrowljansky	37, 39
Aphis subterranea Walker	41
Aphis urticata Fabricius	41
Brevicoryne brassicae (Linn.)	* 41, 82
Capitophorus ribis (Linn.)	39
Cavariella aegopodii (Scop.)	81
Cavariella pastinaceae (Linn.)	34
Cerosipha epilobiina Walker	40
Chaitophorus betulinus van der Goot	40
Hyalopterus arundinis (Fabr.)	41
Macrosiphum barri Essig	*
Macrosiphum obscurus (Koch)	41
Macrosiphum pisi (Kalt.)	x, *, 58, 82, 91, 106
Macrosiphum rosae (Linn.)	x, *
Macrosiphum sanborni Gillette	14, 35, 47
Macrosiphum solanifolii	x, *, 7, 13, 15, 41, 42, 43, 44, 46, 47, 50, 56, 57, 58, 59, 66, 67, 69, 87, 91, 96, 100
Macrosiphum tabaci Pergande	2, 3
Macrosiphum tanaceti (Linn.)	39, 41

TABLE 5 Cont'd

Species	Bibliographical References
Metopeurum fuscovirida Stroyan	40
Metopolophium occidentale Hille Ris Lambers	40
Micromyzus violae (Perg.)	81
Myzus ascalonicus Doncaster	21, 76
Myzus circumflexus (Buckton)	41, 42, 44, 79, 80, 81, 82, 99, 100
Myzus ligustri (Mosley)	39
Myzus ornatus Laing	7, 38, 51, 82
Myzus persicae (Sulzer)	*, 2, 4, 7, 8, 13, 14, 15, 17, 19, 21, 22, 35, 36, 38, 39, 41, 42, 43, 45, 46, 47, 48, 50, 57, 59, 63, 65, 66, 67, 69, 70, 75, 77, 78, 79, 80, 81, 83, 84, 85, 86, 91, 100, 105
Myzus solani (Kalt.)	14, 17, 18, 35, 38, 39, 42, 44, 47, 79, 81, 82
Nasonovia ribicola (Kalt.)	41
Pentalonia nigronervosa Coquerel	55
Rhopalosiphoninus latysiphon (Davidson)	41
Rhopalosiphum conii (David.)	79, 81
Rhopalosiphum fitchii (Sanderson)	*
Rhopalosiphum junackianum (Karsch)	39
Rhopalosiphum maidis (Fitch)	101

TABLE 5 Cont'd

Species	Bibliographical References
Rhopalosiphum nymphaeae (Linn.)	39
Rhopalosiphum rufomaculatum (Wilson)	14
Rhopalosiphum tanacetina (Walker)	41
Rungsia maydis Passerini	40

* reported in this thesis

x reported in this thesis from unpublished work by Dr. Knud G. Swenson