CURRENT STATUS OF BRAMBLE VIRUSES[1]

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Introduction

Virus diseases of raspberries and blackberries are a problem wherever these crops are grown. Over the years our knowledge of the bramble virus diseases has slowly accumulated to the point where some thirty diseases have been described and, for approximately half of these, their mode of transmission has been determined. Since some of the diseases have not been studied critically and comparative studies have not been made between diseases described from the various geographical areas, synonymy can not be assigned with any degree of certainty. Also, as latent viruses are now known to be carried by a number of commercial varieties, investigators often unwittingly described the symptom expression of a complex infection rather than that caused by a single virus. In this paper, I shall endeavour to summarize our current knowledge of the bramble viruses and virus diseases and discuss some of the problems that are in need of additional research.

I MODE OF SPREAD OF BRAMBLE VIRUSES

The viruses in the Rosaceae in general are exceedingly difficult to transmit mechanically. In recent years, some of them have been transmitted to herbaceous test hosts but, in these instances, it is difficult to transmit the viruses back to the original host. Such is the case with the viruses that occur in plants belonging to the genus *Rubus*. Attempts to transmit these viruses mechanically have traditionally failed and it is only within the past few years that a small group of the viruses have been transmitted to herbaceous hosts but attempts to transmit these back to *Rubus* have not succeeded. Thus some vector is probably involved in the transmission of all of the viruses that are known to attack brambles. Vectors for some of these viruses are known but for others the vector has yet to be determined.

Our knowledge of the mode of spread of the bramble viruses was extended rather slowly. Mosaic and leaf curl were shown to be spread by

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the raspberry aphids in 1922. As other viruses were distinguished, aphids were usually found to be vectors. In fact, where the mode of spread was unknown, an aphid vector was usually assumed or implied. It is only within the past decade that our concept of the mode of spread of the bramble viruses has been broadened. As a result of recent European work, we now recognize two other methods of spread, namely by leafhoppers and through the soil.

A. Aphid Transmission

In North America? two species of aphids predominate in all regions where raspberries are grown. These are readily separated in the field; one is large with long legs, commonly called the large raspberry aphid, *Amphorophora rubi* Kalt. The other is small and inconspicuous, commonly called the small raspberry aphid, *Aphis rubicola* Oestlund. When research on the spread of bramble viruses was started in the early 1920's, raspberry aphids were logical suspects as vectors of the two diseases that were known at the time, mosaic and leaf curl. Early workers succeeded in demonstrating that both diseases were spread by the raspberry aphids.

In Europe, the *Rubus* aphids are similar to those in North America. Again two species predominate, *Amphorophora rubi* and *Aphis idaei* v. d. G. Early attempts to transmit bramble viruses in Europe with these two aphids failed repeatedly and it is only within the past decade that they have been shown to be important agents of spread.

Other aphid species occur on wild and cultivated brambles in both Europe and North America but the evidence suggests that these aphids are of relatively minor importance as vectors. The viruses involved are vector specific, those spread by *Amphorophora* spp. are not spread by *Aphis* spp. and vice versa. These vectors are restricted to plants in the genus *Rubus*. For this reason, the natural host range of the aphid-transmitted bramble viruses is very restricted; none has been found in crops outside of the genus *Rubus*.

Aphids that are omnivorous feeders do not generally colonize brambles with the result that the many aphid-transmitted viruses that attack a wide variety of crops are not a problem on brambles. The only one of this type known to occur in brambles is cucumber mosaic virus, which was recently isolated from Lloyd George red raspberry in Scotland (25). The evidence suggests, however, that even this virus is not transmitted from raspberry to raspberry within the field but, having been transmitted to raspberry from some other plant, it may be perpetuated in raspberry by propagation of infected plants.

B. Leafhopper Transmission

Leafhoppers are known to be important vectors of many of the stone fruit viruses hence it is reasonable to consider them potential vectors for viruses of Rubus spp. Leafhoppers are particularly suspect as vectors of those viruses that induce a proliferation of the shoots of affected plants. One such virus disease, called Rubus stunt, is characterized by such symptoms and a leafhopper vector has been demonstrated. The disease was known for many years in Europe but it was not until 1953 that workers in the Netherlands proved that the virus was transmitted by one of the bramble leafhoppers, Macropsis fuscula (Zett.) (21). At the time this work was done, rubus stunt was the only leafhopper-borne virus known from Europe. Bramble diseases similar to Rnbus stunt have been described from North America but none have been shown to be transmitted by leafhoppers. However, the vector of Rubus stunt has been introduced into North America from Europe. At the present time it is restricted to southwestern British Columbia, where it was first found in 1952 (2).

C. Transmission through the Soil

Until 1956, all bramble viruses whose vector had been determined were shown to be spread by insects. For those viruses whose vector had not been determined, it was usually assumed or implied that future investigation would incriminate an aerial vector. Recently, workers in Scotland demonstrated that an important group of viruses that could not be transmitted by the usual vectors were readily transmitted to healthy plants grown in soil taken from a site of a disease outbreak. The main, and perhaps the only infection court for these viruses was the root system. These soil-borne viruses appear to be widely distributed in England and Scotland but, up to the present, they have not been recorded from brambles in North America or from other regions where brambles are grown.

In the raspberry growing areas of eastern Scotland, the most serious virus disease is raspberry leaf-curl. In 1956, Cadman (14) mechanically transmitted a virus from leaf-curl diseased plants to a series of herbaceous test plants. He also transmitted viruses from sugar beet seedlings and weeds growing in the soil where diseased raspberry plants were found. The possible relationships between the viruses isolated from raspberries, sugar beets, and weeds was not known at the time. By means of serological and plant protection tests, these isolates were found to include three distinct viruses, all of which were shown to be transmitted through the soil and to affect brambles. All were thought at first to be undescribed and were given the names raspberry ringspot, beet ringspot, and raspberry yellow-dwarf, Beet ringspot has subsequently been shown to be a strain of tomato black ring and raspberry yellow-dwarf has been identified with Arabis mosaic.

The soil-borne nature of the viruses was demonstrated by growing raspberries and other test plants in soil collected from fields where leaf curl disease occurred naturally. Attempts to render autoclaved soil infective by adding purified virus preparations did not succeed, suggesting that some other factor, presumably a soil-inhabiting organism, is necessary for transmission. Recently, independent experiments in England and Scotland showed that a nematode of the genus Xiphinema behaves as a vector of Arabis mosaic virus (28, 31). The method of spread of the other two viruses has yet to be determined.

II BRIEF SYNOPSIS OF BRAMBLE VIRUSES

A. Aphid-borne

(1) Viruses transmitted by the genus Aphis

Leaf curl (Bennett, 1930)

Leaf curl is restricted to the raspberry growing areas of North America and is more of a problem in the east than in the west. The disease is prevalent in red, purple, and black raspberries, and occurs to a lesser extent on blackberry, dewberry, and wineberry. The characteristic symptoms are curled leaves that are darker green than normal and stunted plants. The virus is transmitted by Aphis rubicola. Two strains are recognized; one affects red raspberry but not black raspberry, the other affects both red and black raspberry.

Raspberry vain chlorosis (Cadman, 1952)

This virus has been described from red raspberry in Scotland by Cadman (2). Characteristic symptom is clearing of the tissue bordering the small leaf veins, the clearing being localized in small, coalesced patches. Cadman demonstrated that the vector in Europe was ~~Aphis idaei~~. In British Columbia most stocks of Lloyd George are infected but there is no evidence of spread to other varieties, Presumably infected stocks were imported from Europe and the virus is merely perpetuated by the propagation of this original stock,

(2) Viruses transmitted by the genus Amphorophora

(a) Mottle viruses; heat labile

Red raspberry mosaic (Bennett, 1932)

The term "red raspberry mosaic" was used by Bennett to apply to a group of symptoms rather than a specific virus, since several viruses or virus strains were considered to be involved. The viruses were symptomless or mild on red raspberry and induced a graduated range of symptoms varying from mild to severe mottling and necrosis in black raspberry. A similar group of viruses has been isolated from red raspberry in British Columbia, all of which are transmitted by A. rubi.

Leaf mottle (Cadman, 1951)

Leaf mottle was the name applied to a virus isolated from European raspberry varieties by Cadman (8). The virus was symptomless or mild in red raspberry but caused necrosis in Rubus henryi and mosaic in R. saxitalis and R. occidentalis, The vector is A. rubi,

Black raspberry necrosis (Stace-Smith, 1955)

This name was applied to a virus in British Columbia that was symptomless or mild in red raspberry but caused severe necrdsis in black raspberry. The virus was identified with a portion of the red raspberry mosaic complex described by Bennett (5). The vector is A. rubi.

Raspberry leaf spot (Cadman, 1952)

Cadman applied the name leaf spot to a virus in red raspberry in Scotland. Most varieties carry it without symptoms but a few develop chlorotic angular spots which frequently coalesce, distorting the lamina. The virus is transmitted by A. rubi.

Thimbleberry ringspot (Stace-Smith, 1958)

This virus occurs in British Columbia on the native thimbleberry, Rubus parviflorus. The evidence suggests that it is restricted to this host. The virus is heat labile. It is transmitted by three aphids that colonize thimbleberry, Amphorophora pnrviflori, Masonaphis dividsoni, and M. maxima,

(b) Yellows viruses; heat stable.

Yellow mosaic (Bennett, 1927)

Yellow mosaic was described as a field disease of black raspberry by Bennett (3) in 1927, and later (5) the same name was applied to a similar disease in red raspberry. Yellow leaves and stunted plants are the symptoms in both hosts. Yellow mosaic is not well characterized in the literature, presumably because most varieties that were grown at the time the disease was studied were infected with viruses of the red raspberry mosaic group, and these viruses influenced the expression of other viruses.

Raspberry yellows (Cadman, 1952)

Raspberry yellows is known to affect only red raspberry varieties (Cadman, 1952). The symptoms are most conspicuous early in the spring, when leaves of affected plants show a vivid yellowing and bronzing of the interveinal areas. Later in the season the chlorosis is less intense and frequently forms a watermark or oak-leaf pattern, The causal virus is heat stable and is transmitted by the aphid A. rubi (Cadman, personal communication).

Rubus yellow-net (Stace-Smith, 1955)

This name was applied to a virus in British Columbia that causes a net-like chlorosis of the foliage of Himalaya blackberry, red raspberry, and black raspberry. The vector is A. rubi. This virus, when combined with black raspberry necrosis virus, induces the mosaic disease in red raspberry (42). A virus corresponding to rubus yellow-net has not been reported from Europe. However, a disease in Europe known as vein-banding is considered similar to mosaic in North America. Preliminary testing in 1958 indicated that a virus comparable to rubus yellow-net is present in veinbanding diseased plants in Scotland (Cadman and Stace-Smith, unpublished).

B. Leafhopper-Transmitted

Rubus stunt (Prentice, 1950)

Rubus stunt was described by Prentice (37) as a virus disease of loganberry, blackberry, and raspberry in southern England. The virus mostly affects blackberries in England, but in the Netherlands a virus that is thought to be the same is a serious problem in red raspberries, The leafhopper, Macropsis fuscula, is the vector in the Netherlands; in England a vector has not yet been determined. Infection in all hosts resulted in the production of numerous, weak canes, giving the plant a bushy appearance. Some infected plants developed abnormal flowers whose floral parts were modified into leaves. Thung (45) reports inactivation of the virus in shoots held at an air temperature of 46°C for two hours.

C. Soil-borne

Raspberry ringspot (Cadman, 1956)

Raspberry ringspot is one of the viruses responsible for the leaf curl disease of raspberries in Scotland. A strain of the virus has also been isolated from raspberries in southern England. The symptoms vary considerably depending upon the variety affected. Some varieties, such as Norfolk Giant, show a severe leaf curling, others show only a ringspot marking of the foliage and a few, such as Lloyd George, appear to be immune. The virus is distinguished from other soil-borne viruses affecting raspberry by the symptoms induced on a series of herbaceous test plants and by serological and plant protection tests.

Tomato black ring (Smith, 1946)

In 1957, Harrison (23) described a soil-borne virus that occurred naturally in several crops and weeds in Scotland. The virus named "beet ring spot" was later shown to be a strain of tomato black ring (24). Raspberry was at first thought to be immune but recently the virus has been isolated from some raspberry varieties (27). Symptoms induced by this virus in susceptible varieties of raspberries differ very little from those caused by raspberry ringspot virus. Diagnosis depends upon the symptoms induced on herbaceous hosts, and upon serological and plant protection tests.

Arabis mosaic (Smith, 1944)

A soil-borne virus of raspberry, strawberry, blackberry and several weed species was described by Harrison (26) in 1958 and provisionally assigned the name "raspberry yellow dwarf". Recent serological and plant protection tests have shown that the virus is the same as Arabis mosaic (28). The virus seems to be widespread in England and rare in Scotland. In raspberry, the virus has been isolated from the variety Malling Exploit, where the characteristic symptoms are vein yellowing and stunting. It was also isolated from a Himalaya blackberry plant showing a yellow mosaic pattern in its leaves.

D. Vector Undetermined

Black raspberry streak (Wilcox, 1922)

This disease of black raspberry was described in 1922 (47) but the virus nature was not determined until 1948 (29). The disease is recognized by the discolored streaks that develop on the canes. The intensity of the streaking varies considerably, which suggests the existance of strains. An insect vector has usually been assumed but no vector has been demonstrated.

Blackberry dwarf (Zeller, 1927)

In 1927, Zeller (50) described a disease of Phenomenal berry and loganberry in Oregon which he called blackberry dwarf. Infected plants had thin canes with short internodes and an increased number of buds at each node, Leaflets were small, distorted, and mottled. A natural vector was not determined, although one of the rose aphids, Capitophorus tetrarhodus, was able to transmit the disease under caged conditions,

Yellow-blotch curl (Chamberlain, 1938)

This virus disease was described from Ontario, Canada, in 1938 (18). Diseased plants showed reduced vigour with the leaves curled down and blotched,

Necrotic fern-leaf mosaic (Chamberlain, 1941)

This virus disease was described from Ontario, Canada, in 1941 (19). Symptoms were mottled, necrotic leaves, retarded foliation, and general stunting.

Raspberry decline (Zeller & Braun, 1943)

Decline is a disease of red raspberry in Oregon (51). Diagnosis depended upon field observations, where infected plants progressively deteriorated over a maximum of about 3 years. A virus was thought to be responsible for this deterioration.

Blackberry variegation (Horn, 1948)

Blackberry variegation occurred in a single wild blackberry plant in Maryland (29). The virus was transmitted by grafting to blackberry: and black raspberry. In both hosts, varying degrees of chlorosis developed on the leaves of affected plants.

Loganberry dwarf (Wilhelm et al., 1948)

This disease primarily affects loganberry and related hybrids in California (48). Diseased plants have dwarfed canes, weak fruiting laterals, and precociously developed basal buds, giving the plants a bunchy appearance late in the season,

Curly dwarf (Prentice & Harris, 1950)

Curly dwarf was described in 1950 (38), occurring as a latent virus in Lloyd George raspberry in England. The virus was detected by grafting to the indicator variety Baumforth B, in which leaf curling and dwarfing were induced,

Ringspot (Vaughan et al., 1951)

Ringspot is a virus disease of red raspberry in Washington and Oregon (46). Infected plants show ringspot markings of the foliage. There is no indication that this virus is related to the soil-borne ringspot viruses of Scotland,

Bushy dwarf (Cadman & Harris, 1951)

Bushy dwarf was the name applied to a disease of Lloyd George raspberry in Britain (7). Symptoms are dwarfing of the canes and down-curling and chlorosis of the leaves.

Raspberry yellow-blotch (Cadman & Harris, 1952)

This name was applied to a disease of Lloyd George raspberry in Scotland in 1952 (16). Affected plants showed a coarse yellow blotching of the lower leaves of the young canes and necrosis of the fruiting canes. The causal virus was thought to be transmitted by Amphorophora rubi but it is now considered doubtful that this aphid is in fact a vector (Cadman, personal communication).

Blackberry mosaic (Alcorn et al., 1955)

This disease of Himalaya blackberry was described from California in 1955 (1). Infected plants showed a marked reduction in size and number of leaflets, the length and diameter of the canes. Leaves exhibited a variety of mosaic symptoms. The authors suspected that at least two component viruses were involved.

Loganberry degeneration (Legg, in press)

Loganberry degeneration is the name proposed by Legg (35) for a virus detected in weak loganberry plants in England. It causes symptoms in R. henryi but not in other indicator hosts tested.

III VIRUS-VECTOR RELATIONSHIPS

Aphid-transmitted viruses may be usefully divided into three groups: nonpersistent, semipersistent, and persistent, but the modern concept is that the virus-vector relationships form a continuum (44). The nonpersistent viruses can be acquired and transmitted in a few seconds; the semipersistent and persistent viruses require minutes or hours to acquire and transmit. The nonpersistent viruses are rapidly lost by the aphids, usually within minutes; the semipersistent viruses are retained for hours instead of minutes, and the persistent viruses are retained for days or weeks. In order to determine vector relations, virus, vector, and test plant have to be combined so that a reasonable degree of transmission can be achieved, For many of the aphid-transmitted bramble viruses this combination has not been determined with the result that their virus-vector relations are not known.

In North America, the vector relations of raspberry leaf curl, transmitted by Aphis rubicola, is not well understood, Bennett (3) reported transmission experiments which showed that the virus was acquired by the aphids within two hours and that aphids remained viruliferous for a considerable time, possibly for the life of the aphid. In determining the retention of the virus, aphids were held for varying periods on a raspberry variety that was thought to be immune to the virus, The possibility exists that some multiplication occurred in the apparently immune host and that the aphids lost their virus in a relatively short time and then acquired a new charge of virus. Thus, although the variety may have been immune, further work should be done before drawing conclusions on the vector relations of the virus.

The vector relations of the other virus known to be transmitted by aphids belonging to the genus Aphis, raspberry vein chlorosis, is also not well known, mainly because red raspberry, which has been used as a test host, is difficult to infect. In Scotland this virus was shown to be transmitted by Aphis idaei but no information was obtained about its vector relations.

For those viruses transmitted by Amphorophora rubi, the evidence suggests that most, and possibly all, are semipersistent. The mild or latent viruses have approximately the same vector relations. One that has been studied in detail, black raspberry necrosis virus, is acquired by the aphid within 30 minutes, inoculated within 2 minutes, and persists in the feeding aphid for only a few hours. When the aphids are starved, they can retain the virus for at least one day at 20°C and at least 4 days at 3°C. Fasting before acquisition has no effect on the length of the acquisition feed required. The vector relations of the yellows type viruses do not differ appreciably from the latent viruses. Yellow mosaic is acquired within 2 hours and retained by some aphids for more than 12 hours but less than 24 hours (5). Vector relations of raspberry yellows are not known. Yellow-net is acquired within 1 hour, transmitted within 15 minutes, and usually persists less than 4 hours. Starved aphids may retain the virus for 1 day when held at 20"C. and 4 days when held at 3°C. The following table summarizes the vector relationships and other features of a heat labile and heat stable virus transmitted by Amphorophora rubi.

Table 1

CHARACTERISTICS OF TWO APHID-TRANSMITTED VIRUSES

Property	Black raspberry necrosis virus	Rubus yellow-net virus
Heat tolerance	labile	stable
Tissue affected	mesophyll	phloem
Incubation time	1 week	3 weeks
Vector relationships		
Acquisition feeding time	<30 minutes	<1 hour
Effect of preliminary fasting	none	none
Latent period	none	none
Inoculation time	2 minutes	C 15 minutes
Retention-feeding	1-2 hours	1-2 hours
fasting (at 20°C)	1 day	1 day
(at 3°C)	4 days	4 days

The bramble viruses that are transmitted by Amphorophora rubi agree in most essential details with the characteristics of the semipersistent viruses as outlined by Sylvester (44). The only difference is in the retention of the virus while the aphid is fasting, With the bramble viruses the virus is retained considerably longer in the fasting aphid than in the feeding aphid whereas with beet yellows: the semipersistent virus investigated by Sylvester, the reverse was true.

One problem in the study of bramble virus diseases is that the viruses transmitted by Amphorophora rubi have approximately the same vector relations, with the result that virus complexes are not readily separated. Many field diseases are caused by the combined effect of two or more unrelated viruses and mass transfer of aphids to test plants do not result in a separation of the component viruses. An example of this is raspberry mosaic, which in British Columbia was shown to be caused by the combined effect of black raspberry necrosis virus and rubus yellow-net virus. When several aphids are transferred from a mosaic diseased plant to a black raspberry indicator plant, the two viruses are simultaneously transmitted and the symptoms of black raspberry necrosis virus, which develop in 5 to 7 days, completely obliterate the symptoms of rubus yellow-net, which require about three weeks to develop. However, when single aphids are transferred to a series of test plants the two viruses may be separated by chance,

The vector relations of the leafhopper transmitted virus, Rubus stunt, have been investigated by de Fluiter and van der Meer (22). Preliminary work indicates that the virus has a latent period of more than 8 days and persists in the vector for more than a month.

IV PROBLEMS IN VECTOR IDENTIFICATION

A knowledge of the biology of the vectors is essential in devising sound control procedures yet our understanding of the vectors of the bramble virus diseases is deficient in many respects. In fact, for about one half of the diseases that have been described no vector has bean determined. Admittedly some of these diseases are of local significance and minor economic importance but others, such as black raspberry streak, are of major concern. Thus one of the greatest needs is far the discovery of the vector of those viruses whose mode of spread is unknown, not only from the control aspect but also as an aid in the identity of the causal virus and its relationship to other known bramble viruses.

Much remains to be learned about the taxonomy and biology of the aphids that are known to be impostant as vectors. Most vector studies have been undertaken by plant pathologists so that purely entomological aspects have been neglected. A weakness of much early work lies in the doubtful identity of the aphids tested. For example, in early tests the large raspberry aphid was not distinguished from the small raspberry aphid with the result that Aphis rubicola was for several years erroneously considered to be the vector of mosaic. We now recognize the prime importance of accurate identification but taxonomic studies on the Rubus-inhabiting aphids must proceed further before definite determinations are possible.

Speciation in the bramble aphids appears to have proceeded further in North America than In Europe; so that identification is more of a problem here than in Europe. Twelve species of bramble aphids of the genus Amphorophora have been described in North America whereas in Europe only one is recognized. Some of the North American species are now placed in Masonaphis, and the validity of others was recently questioned by MacGillivray (36). According to the literature, A. rubi occurs on many wild and cultivated species of Rubus. Evidence from British Columbia suggests that this is not so, Amphorophora rubi is almost entirely restricted to cultivated forms of raspberry and blackberry, but other aphids, morphologically similar, occur on wild Rubus species. One in British Columbia, Amphorophora rubitoxica, occurs on black raspberry, loganberry, and the wild trailing blackberry but will not colonize red raspberry. Another, Amphorophora parviflori, is restricted to the wild thimbleberry. Neither of these aphids is able to transmit the common raspberry viruses.

In the genus Aphis, two species are recognized in North America, rubicola and rubifolii. These two species are morphologically so similar that the diagnostic character used to separate them is the number of antennal segments; rubicola has 6 while rubifolii has 5. Some authors consider that rubicola is the raspberry aphid and does not occur on blackberry, whereas rubifolii occurs on blackberry but not on raspberry, Other authors, however, report collections of both species on red raspberry. This contradictory evidence may be explained by unreliable morphological characteristics used to separate the two species. According to Hille Bis Lambers (personal communication) a separation of these two species based upon the number of antennal segments is not reliable.

A more detailed study of the taxonomy,' host orange, and vector potential of the various bramble aphids is essential. Our progress has been hindered in the past because plant pathologists and entomologists have worked in isolation. Surely a teamwork approach is called Pop.

V TRENDS IN CONTROL OF BRAMBLE VIRUSES

The development of sound measures to control the spread of bramble viruses depends upon an understanding of the mode of transmission and the biology of the vector. Particular attention has been paid to controlling raspberry mosaic, probably the most widespread and destructive of the bramble virus diseases. Certification programs have bean established in most raspberry growing regions to provide propagators with relatively clean stock. These schemes have been only partially effective, however, and indiscriminate propagation of planting stock is still commonly practiced, More lasting control involves breeding varieties resistant to the aphid or to infection by the aphid. This is generally recognized as the most satisfactory method of control.

In North America, the variety Herbert was used as a parent in raspberry breeding as early as 1922, since this variety had an obviously low incidence of mosaic in commercial plantings. It was later demonstrated by Winter (49) that the vector, Amphorophora rubi, did not feed or reproduce readily on this variety, Similarily, Lloyd George has remained relatively free of mosaic since its introduction into North America from Europe in 1926, a characteristic that has made this variety a favored parent in raspberry breeding. Schwartze and Huber (39) demonstrated that Lloyd George was resistant to Amphorophora rubi and that the factors controlling resistance were carried by 2 or more genes.

In Britain, workers at East Malling have recently undertaken a thorough study of the genetics of resistance to Amphorophora rubi in the raspberry. Resistance in the variety Baumforth A was shown to be controlled by a single dominant gene, designated A_1 (33). The American variety Chief was shown to carry six dominant genes for resistance, which were designated A_2 to A7 (34). Work presently in progress has shown that the American black raspberry R. occidentalis L. provides a valuable source of resistance and that a number of other sources are available (Knight, personal communication). Thus in Britain there is every indication that genes for aphid resistance can be incorporated into new varieties.

The Lloyd George variety has remained relatively free from mosaic in North America whereas the same variety is very susceptible to mosaic in Europe. At first this led to speculation that the viruses involved in the disease in North America were distinct from those in Europe. However, it was noted that the aphid vector refused to breed on Lloyd George in North America although in Britain large populations were found on this variety; hence it was concluded that two strains of the aphid exist, one in North America and one in Europe. These were the only strains of Amphorophora rubi known on raspberry until 1958 when, as an important by-product of the raspberry breeding project in England, three strains were discovered (6). More recently, a fourth strain has been discovered in England. Sources of resistance are known against all of these strains. (Briggs, personal communication).

Obviously the success of a control program based upon varieties resistant to the vector depends upon the stability of the vector. If A. rubi is capable of mutating and developing new strains that would attack varieties that were resistant when released, a control program based on breeding for resistance would be of little lasting value. Data available suggests that the aphid is stable and that resistance will withstand the test of time. The best example is the Lloyd George variety which has been grown in the Pacific Northwest for over thirty years and has remained resistant to Amphorophora rubi.

Resistance of raspberry varieties to infection with viruses carried by *Amphorophora rubi* is not dependent solely on resistance to the vector. In addition, a true resistance to infection is recognized, although the nature of this resistance is not understood. In Scotland, Cadman and Fiskin (17) found that raspberry varieties differed greatly in susceptibility to infection by aphid-transmitted viruses and that the differences were not correlated with aphid resistance. In North America most varieties that are reported to escape mosaic infection are either fully immune or partially resistant to the aphid vector. A variety such as Washington, however, supports a moderate aphid population and yet plants of this variety are rarely infected in the field and are difficult to infect in the greenhouse where viruliferous aphids are transferred directly from the diseased source plants. The possibility of utilizing resistance to infection as opposed to resistance to the vector is being explored at East Malling by Knight and Keep (32).

Limited evidence suggests that the genes for resistance to the American strain of *Amphorophora rubi* have their origin in the European red raspberry, *Rubus idaeus*, whereas resistance to the European strains have their origin in the American red raspberry, *Rubus idaeus* sub-species *strigosus*. In North America, all varieties that have been reported to be resistant are of European origin while in Europe resistant varieties are derived in part at least from the American red raspberry.

Another technique that may serve a useful function in controlling aphid-transmitted viruses is heat therapy. Chambers (20) has reported inactivation of latent viruses in Scotland by holding raspberry plants from 1 to 4 weeks at an air temperature of 32°C. Similar results have been obtained in British Columbia. Black raspberry necrosis virus and other latent viruses in red raspberry plants have been successfully eliminated from plants held at an air temperature of 37°C for periods ranging from 5 to 10 days. Two other viruses, rubus yetlow-.net and raspberry vein chlorosis were not eliminated from plants so treated for periods up to 3 months, This limited evidence suggests that bramble viruses may be usefully divided into two groups, the heat labile and the heat stable, depending upon their ability to withstand heat treatment. This technique is particularly valuable for virus identification and for obtaining a virus-free clone of some of the older varieties that have become universally infected with latent viruses.

Breeding for resistance has not been attempted to cnntrol the leafhopper-borne virus disease, **Rubus** stunt. In the Netherlands, however, satisfactory control has been achieved with insecticides. In fact, the rapid increase in the incidence of **Rubus** stunt beginning about 1945 has been correlated with a change in spraying materials. Prior to 1945, raspberries were sprayed with dormant tar oils to control a variety of insects and this material must have destroyed the eggs of the vector. Subsequently DDT replaced tar oils and, although it controlled other pests, it had little effect on M. fuscula with the result that high populations developed and the virus spread proportionately. Spray programs are now directed against the leafhopper and this has resulted in a marked reduction in the incidence of Rubus stunt (22).

Too little is known about the distribution and means of spread of the soil-borne viruses but they pose difficult problems not encountered in the control of viruses with aerial vectors, Rotating crops and propagating virus-free stock under isolated conditions are not effective since the viruses are carried in a wide variety of crop and weed hosts. The most promising measure involves planting varieties that appear to be immune. Lloyd George, for instance, is immune from raspberry ringspot and tomato black ring but susceptible to Arabis mosaic. Malling Jewel is immune from Arabis mosaic but susceptible to the other two. Sources of resistance are thus known and it is probable that the genes for resistance could be combined in breeding resistant plants.

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