Leafhopper Vectors and Plant Disease Agents

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ACADEMIC PRESS New York San Francisco London 1979

A Subsidiary of Harcourt Brace Jovanovich, Publishers

Chapter 3

LEAFHOPPER AND PLANTHOPPER VECTORS OF PLANT DISEASE AGENTS IN CENTRAL AND SOUTHERN EUROPE

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ISBN 0-12-470280-5

3.1 INTRODUCTION

Most of the subjects dealt with in this survey summarize investigations that were done as a consequence of heavy losses in crop plants due to either leafhopper or planthopper-vectored viruses or mycoplasmalike organisms. In my native country these investigations concerned e.g. a variation of the stolbur disease, the study of which started further detailed investigations of other mycoplasma diseases and the epidemic oat sterile dwarf virus diseases that initiated thorough research of virus and mycoplasma diseases of cereals. Historically, some of these or similar plant diseases were observed long before viral and mycoplasma eitology of plant diseases were understood. Mycoplasma symptoms in plants were noticed, probably for the first time, by the Italian scientist and professor Ulisse Aldrovandi (+1605) in Bologna, who published the illustration of virescence in Aquilegia in 1642 (Grancini, 1962). Engelmann's *"De antholysi prodromus"* (Frankfurt a/M., 1832) contains descriptions of greening and phyllody symptoms, as mentioned by Blattny (1957) who also noted that a disease of scarlet pimpernal, now known to be caused by mycoplasma, was observed by botanists in Czechoslovakia 160 years ago. The European aster yellows disease was reported in Germany in 1935.

This review is a summary of various points of view from several monographs, surveys and bibliographies, e.g. by Heinze (1959), Nielson (1968), Ishihara (1969), Maramorosch *et al.* (1970), Marchoux *et al.* (1970), Brčák (1971), Fritzsche *et al.* (1972a), Harpaz (1972), Horváth (1972, 1974), Kisimoto (1973), and Müller *et al.* (1975). Nevertheless, only a few planthopper and leafhopper species have been shown to be vectors of plant viruses and mycoplasmas, especially in Europe, where mostly only the most abundant species were examined.

In some cases, species introduced from another continent were examined to determine their vector ability, although they were not reported plant disease vectors in their native home. For example, *Fieberiella florii* (Stål) was shown to be a vector of some mycoplasmas in North America thirty years ago by Severin (1947); however, in its palearctic home, no one demonstrated an interest in showing its relations to similar European diseases. *F. florii* also occurs, e.g., also in warm regions of Czechoslovakia (Dlabola, 1954) and in Bulgaria (Pelov, 1968). Contrariwise, *Scaphoideus littoralis* Ball was introduced from North America into southwest Europe, where it transmits *flavescence dorée* of grapevines, but nothing has been reported on its ability to transmit mycoplasmas in North America. Some additional holarctic species of vectors were studied more thoroughly in North America than in Europe. For instance, in North America the froghopper, *Philaenus spumarius* Linné, is a vector of Pierce's disease of grapevines. In Europe a similar disease occurs: namely, the infectious necrosis of grapevines, apparently caused by an agent resembling rickettsia (Ulrychová *et al.*, 1975). Its vector in Europe is not yet known. On the other hand, a remarkable piece of research was published by Maramorosch (1958, 1960) who showed that the North American species *Macrosteles fascifrons* (Stål) was also able to transmit a European agent of aster yellows, while the usual European vector of this disease agent, *Macrosteles laevis* (Ribaut), did not transmit two American strains of aster yellows.

Some records from certain parts of Euroasia remained neglected, although they dealt with species occurring in central and southern Europe as well. In other countries, no one has demonstrated the vector capabilities of *Peragallia sinuata* (Mulsant and Rey) and *Anaceratagallia venosa* (Fourcroy) reported from the U.S.S.R., *Javesella obscurella* (Boheman) from Finland, *Muellerianella fairmairei* (Perris) from Japan, or *Circulifer opacipennis* (Lethierry) which occurs in Mediterranean and other south-European areas.

After 1967, a hasty revaluation of the etiology of yellows diseases occurred, based mostly only on electron microscopy and chemotherapy (Doi *et al.*, 1967; Ishiie *et al.*, 1967). Previously, many authors were puzzled with strain differentiation of yellows agents and with their classification. Krieg (1961), for example, suggested a new class of viruses, Arthropodophaga, in which he included the order Arthropodophiliales; a new suborder Phytovectales; a single (new) family, Homopterophilaceae; and the genera *Chlorogenusvirus* (yellows) and *Aureogenusvirus*. The latter genus included agents of wound tumor, clover club leaf, and potato yellow dwarf diseases. Incorrect classifications like this arose as a consequence of incomplete knowledge of the pathogens. In spite of this, many authors retained a noncomittal attitude. Bos and Grancini (1965) discredited species classification of yellows agents that had only small differences in symptoms and some vector specifities. However, certain conclusions could be drawn from comparative studies of extensive materials. Valenta (1964) investigated over 200 isolates of yellows agents and showed that at least four entities could be distinguished: stolbur, parastolbur, clover dwarf, and clover phyllody (having four distinct types). Electron microscopy that was used to demonstrate the presence of prokaryotic plant pathogens both in host plants and vectors affected with yellows diseases was ineffective in the differentiation of these agents (Maramorosch *et al.*, 1970). Those simplest prokaryotes were usually called mycoplasmas (or mycoplasmalike organisms, MLO's), which, of course, was not sufficiently warranted. Despite this, the term has been maintained. Bodies resembling MLO's were observed in insect species that were unable to transmit any plant disease (cf.e.g. Maillet *et al.*, 1968; Devauchelle *et al.*, 1969). Regardless, many mycoplasmatologists disagreed with the use of the

term "mycoplasma" for prokaryotic plant pathogens. Furthermore, I am afraid further unsolved "species and strain" problems will occur even in situations in which plant pathologists will be able to fulfill the minimum standards for description of new species as postulated by Maramorosch (1972) or Edward *et al.* (1972). A similar situation exists with descriptions of some groups of plant viruses, the common names of which regretably play a more important role than a precise knowledge of their properties.

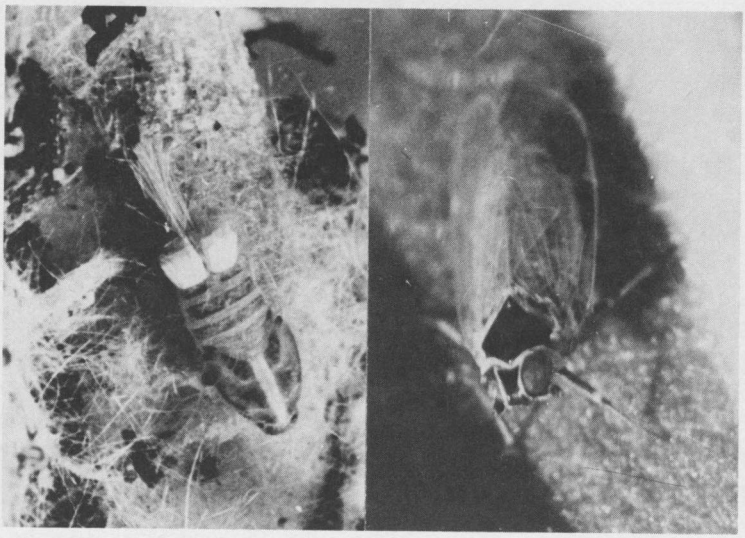
The present survey does not include possible relationships of rickettsianlike organisms (RLO) found in diseased plants, as well as in insect vectors and nonvectors as well. These disease agents were originally observed by Swezy and Severin (1930). Rickettsialike structures were observed in leafhopper vectors by Nasu (1965) and Marmaorosch *et al.* (1968) who suggested that these structures probably were symbiotic species or parasites (Maillet, 1971). The only etiological importance of rickettsialike organisms (RLO's) in host plants and vectors in Europe was the finding of RLO and MLO simultaneously both in dwarfed, proliferated carrot plants and in the vector of these disease agents, the psyllid *Trioza nigricornis* Forst. (Giannotti and Vago, 1974; Giannotti *et al.* 1974). I will not discuss all findings of RLO's in plants in Europe, because no leafhopper or planthopper vectors of the respective diseases are known.

Of course, we cannot claim that MLO's and RLO's observed in insect tissues are the causal agents of plant diseases in all cases. Prokaryotic plant pathogens were shown to survive for certain periods in insects that were unable to transmit them. Kleinhempel *et al.* (1974) injected an *Acholeplasma* isolate, obtained from white clover and cultivated in bouillon medium, into various insects and stated that this agent survived not only in *Euscelis plebeja* (Fallén) but also in the bug *Piesma quadratum* Fieb. (30 days) and in the beetle *Phyllotreta* sp. (25 days. Other plant pathogens may survive in nonvector species. Ossiannilsson (1958) identified tobacco mosaic virus (TMV) particles in alimentary tract of leafhoppers, *Cicadella atropunctata* (Goeze), previously fed on TMV diseased plants.

Some treatises on individual vectors included information dealing with control of plant diseases spread by leafhopper vectors. A list of special problems in this field were compiled by Fritzsche *et al.* (1972b) and a general view of control measures was presented by Heathcote (1973). Some leafhopper transmitted viruses infect many wild plants that function as virus reservoirs. Wild plants may be the principal hosts for many MLO's as well. Infected crop plants often play no or an unimportant role in further spread of yellows diseases (Valenta, 1968). Furthermore, it might be interesting to compile a list of leafhopper species that are nonvectors of mycoplasma diseases. A comparison of these with known vectors would possibly show that the insect vector host range is rather limited. In connection with ideas mentioned above, an interesting attempt was made by Valenta and Musil (1966) who serologically proved taxonomic relations of *Aphrodes, Euscelis,* and *Macrosteles* leafhoppers.

It would be worth comparing the multiplication of viruses and mycoplasmas in various vector species. Some of these agents appear to multiply faster in insects than in plants. Of course, it is not possible to develop an unbiased basis enabling a comparison of insects and plants as hosts even if we would merely evaluate the rate of pathogen multiplication and pathological effects in both host organisms. Some authors (Maramorosch, 1954; Harpaz, 1972) suggested the hypothesis that plant pathogenic MLO's and some viruses might be insect pathogens, primarily, which later extended their host range to plants. This idea warrants additional discussion. Pathogens which have been associated with their hosts for a long time usually do not act in as aggressive a manner as with new hosts. An apparently larger MLO host range in plants as opposed to insects might seemingly contradict the above hypothesis. However, some plants species infected only experimentally, may show mild symptoms similar to reactions of viruses in tolerant and latent hosts (e.g. *Nicotiana glauca* Grah. infected with the potato witches' broom mycoplasma). Similar tolerant reactions, such as a long latent period and no apparent alterations of host development and behaviour, can be observed in some vectors of MLO's. Thus, the hypothesis regarding primary and secondary hosts of plant viruses and MLO's promotes speculation and no generalizations can be made.

Vector transmission of MLO's is similar to transmission of propagative viruses in many respects. Nevertheless, the role of pathogen stages in host plants that may influence acquisition of the disease agent by the vector is poorly understood. A relatively long minimum acquisition access may be due to peculiarities of the disease agents within the plant sources. Similarly, the infection process of MLO's



Figs. 1 and 2. A female and a nymph of *Hyalesthes obsoletus* Sign. (photograph by J. Brčák).

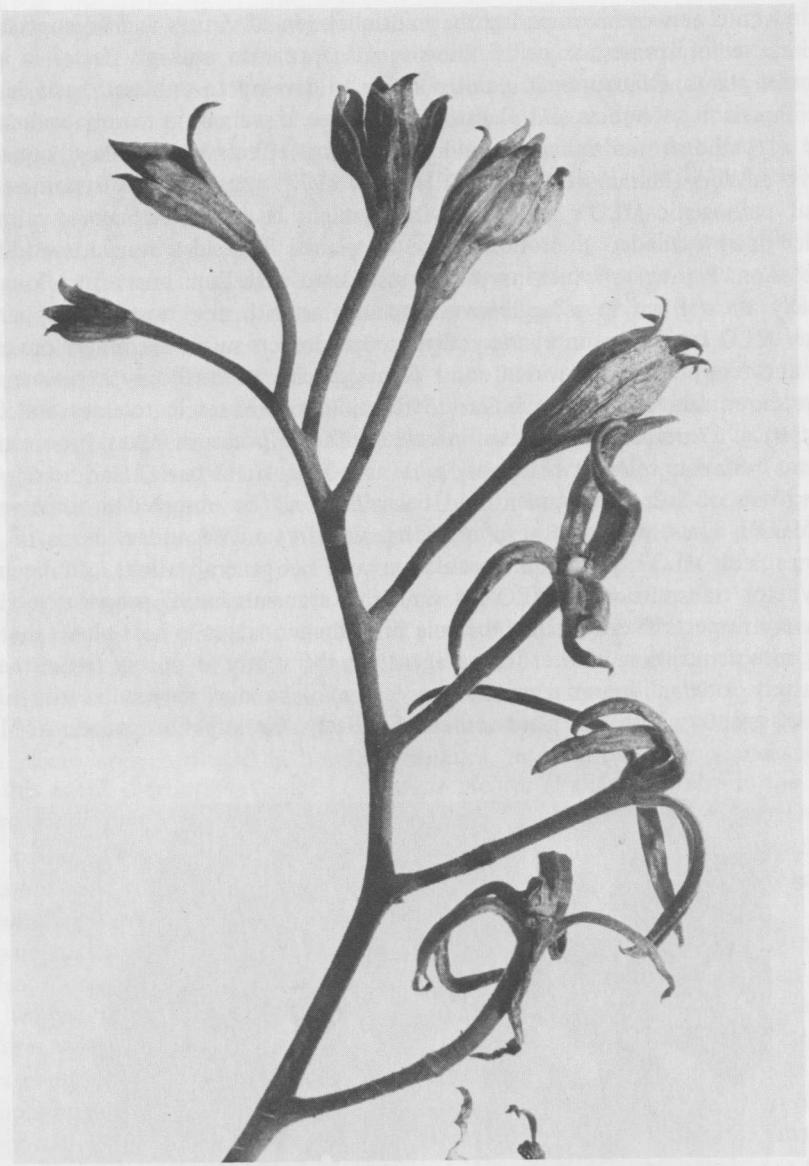


Fig. 3. Natural stolbur infection of a tomato plant (photograph by J. Brčák).

within vectors may reflect interference phenomena.

The next part contains a survey of leafhopper species in Homoptera (Auchenorrhyncha) that are known vectors of virus and MLO disease agents of plants in

central and southern Europe. Additional details published in well known monographs are discussed briefly.

3.2 *Hyalesthes obsoletus* Signoret

This species is known to transmit only a single MLO that causes stolbur (Figs. 1-3). The first report was published in the U.S.S.R. by Suchov and Vovk (1946) who called this disease the southern stolbur. This disease was described and the infectivity of vector was confirmed experimentally in Czechoslovakia by Brčák (1954), Valenta and Musil (1956), and Valenta (1958); in Bulgaria by Kovačevski (1956), Kovačevski *et al.* (1964); and in Roumania by Ploaie (1960). The MLO etiology of the stolbur disease was first reported by Ploaie and Maramorosch (1969).

The distribution of *H. obsoletus* based on the knowledge of that time was compiled by Blattný *et al.* (1954). The northern limits of *H. obsoletus* distribution extended from Portugal, Spain, France, Germany, Czechoslovakia, Roumania, north of Black Sea and eastward beyond the Caspian and Aral Seas. The most southern occurrences of *H. obsoletus* were noted from Algeria, Tunisia and from Israel, Syria, and Iraq and near Aschabad to the East. *H. obsoletus* prefers dry and warm conditions. The correlation of its distribution in Bohemia and Moravia with the occurrence of the stolbur disease was studied in more detail by Brčák (1955) and Brčák *et al.* (1955). In Slovakia, Valenta (1953) stated that the northern limits of *H. obsoletus* occurrence agreed with the distribution of the xerophyte grass species *Bothriochloa ischaemum* Keng. Blattný *et al.* (1954) reported the presence of *H. obsoletus* and stolbur in dry districts which were or might be suitable for vineyards. In the vineyard area of Switzerland, Bovey (1956) found in 1953 a previously unrecorded disease of tomatoes symptomatically related to stolbur. Stolbur disease has also been reported in Austria (Wenzel, 1956). In Roumania, stolbur and *H. obsoletus* occur in plain regions (Ploaie, 1960).

H. obsoletus has only one generation a year. It overwinters as fourth instar nymphs. Adults appear during the second half of June and live as long as 43 days (Kovačevski *et al.*, 1964a). The egg stage develops for 22 to 46 days (Kovačevski, 1964), a female lays an average of 60 eggs (Musil, 1956). The maximum occurrence of adults is usually during the first third or half of July (Săvulescu and Ploaie, 1964; Kuroli, 1970), when adults begin to migrate from primary host plants to other plant species. This migration extended over a long period plays the main role in the spread of stolbur. This migration was considered to be a natural phenomenon caused presumably by needed exchange of hosts. However, it was shown that a greater part of *H. obsoletus* population did not migrate at all and stayed on its primary host plants (Valenta, 1956). During colder summers and in colder districts, Brčák (1955, 1958) and Brčák *et al.* (1955) observed that *H. obsoletus* did not leave its primary host plant, *Convolvulus arvensis* L., at all, provided this plant remained fresh and suitable for feeding by adults. No transmission of stolbur to crop plants was reported in such cases.

In central Europe, the bindweed (*Convolvulus arvensis* L.) represents the main host plant of *H. obsoletus*. Bindweed plants are also a natural source of the stolbur agent (Razvjazkina, 1950; Valenta, 1953; Kovačevski, 1956; Bojňanský *et al.*, 1975). Nymphs of *H. obsoletus* feed on underground parts of bindweed plants, usually at a depth of 7 to 12 cm, but during cold periods they were found even 30 to 35 cm deep in the soil (Kovačevski, 1958). Five nymphal instars of *H. obsoletus* were described by Musil (1956). Nymphs of *H. obsoletus* are able to develop on other plant species. In France, Leclant (1968) and Moreau and Leclant (1973) observed that *H. obsoletus* accomplished its entire biological cycle on lavander. Also, Leclant and Lacote (1969) reported that in southern France *H. obsoletus* was found in great numbers only on roots of lavander and never observed on roots of bindweed, although this plant was infected with stolbur. Kovačevski (1958) found nymphs of *H. obsoletus* feeding on *Lepidium draba* L., *Amaranthus retroflexus* L., *Chenopodium album* L., *Cirsium arvense* Scop., and *Solanum tuberosum* L. Adults of *H. obsoletus* are polyphagous, but apparently they prefer bindweed and perhaps even stolbur infected bindweed (Brčák, 1955). Among crop plants, potatoes were frequently infested with considerable numbers of adults (Brčák *et al.*, 1955). In Bulgaria adults of *H. obsoletus* were infrequent on tomatoes, red pepper, eggplant, potatoes and bindweed; nevertheless, they occurred frequently even in plants not suffering from the stolbur disease, e.g. maize, soybean, castor bean, sesame, *Amaranthus retroflexus* L., *Chenopodium album* L., *Hyoscyamus niger* L., *Cirsium arvense* Scop., *Sambucus ebulus* L., etc. (Kovačevski, 1958).

Under natural conditions, stolbur initially occurs in foci (Valenta, 1953, 1956). Natural foci of infection serve as infection sources having a stable trophic relationship to vectors which migrate from them. Thus, its vector and host reservoir plants can exist for an unlimited period. After mating, *H. obsoletus* leaves bindweed plants for other plants to which it transmits the stolbur agent. Mass migrations can be observed especially in warm southern areas (Brčák, 1958); whereas, in colder areas where bindweed plants remain fresh even in summer, most of *H. obsoletus* population remains on bindweed (Brčák, 1955). Valenta (1956) observed that even in natural foci of stolbur a considerable part of *H. obsoletus* populations do not leave bindweed. In this way, the stolbur agent is transmitted from weed to weed, insuring the maintainance of infection foci. Thus, stolbur exists independently of crop plants. Valenta (1956) also observed stolbur foci in semisteppe pastures, where the natural infectivity of *H. obsoletus* reached up to 24 per cent and where regular contacts with crop plants could hardly be presumed. Blattný *et al.* (1956) studied small natural foci of stolbur in central Bohemia that consisted of stolbur-diseased bindweed plants and low population of *H. obsoletus*. No stolbur infected crop plants were found in proximity of those foci. However, tomato seedlings planted into those foci became naturally infected (Fig. 3). Brčák (1958), in Bohemia, discovered small stolbur foci having only few infected bindweed plants and no *H. obsoletus*.

Stolbur disease occurs abundantly only in some years (Panjan, 1958; Bojňanský and Kosljarová, 1962; Gáborjányi and Sáringer, 1967). Kuroli (1970) observed

that a decrease in stolbur was proportional to the occurrence of *H. obsoletus*. In the areas of Hungary studied, 5 to 15% of tomato and pepper plants were infected in 1967, and only 0 to 1% in 1970. In Bulgaria, Kovačevski *et al.* (1964a) observed an abundance of *H. obsoletus* until 1954. Later, its population density decreased considerably. In Slovakia, the problem of stolbur incidences and forecasting were studied by Bojňanský and Kosljarová (1962). They concluded that dry and warm weather in April, May, and June strongly influenced the vector *H. obsoletus*. Years of high stolbur incidence are characterized by poor rainfalls in June and July and a mean temperature of 2°C higher from April to September. Frosts without snow and sudden temperature changes during winter destroy some infected bindweed plants. From 1948 to 1955, there was significant culmination of stolbur disease incidence in warm areas of Czechoslovakia, where 50 to 100% of potato plants were infected. A proportional increase was observed in *H. obsoletus* populations. Bojnansky *et al.* (1975), using old records on potato degeneration apparently caused by stolbur, reported three destructive epidemics of stolbur in 1921-24, 1932-34, 1948-55, and less severe epidemics in 1963-64. They also developed a method for stolbur forecasting based on a coefficient compiled from the mean sum of monthly temperatures and rainfalls between April and June.

Currently, we ought to term stolbur a disease occurring in the U.S.S.R. like the so called southern stolbur (Suchov and Vovk, 1949), that is transmitted by *H. obsoletus* and other leafhoppers. The differences between stolbur disease and some other yellows diseases were given by Valenta *et al.* (1960). Stolbur was recorded for the first time in Czechoslovakia in 1932 (Valenta, 1953). Besides the countries already mentioned, it was thoroughly investigated in Yugoslavia (Panjan, 1958; Aleksić *et al.*, 1967, 1968; Klindić and Buturović, 1959). Belli *et al.* (1972) reported the occurrence of stolbur from central and southern Italy, but its vectors were not investigated there.

Potato, tomato, red pepper, and tobacco are usually very susceptible to stolbur. Valenta (1953) reported total field infections of tomatoes and 90% infection of potatoes. The correlation of the occurrence of stolbur and *H. obsoletus* was not reported in every case. For example, some annual plants showed early stolbur symptoms, thus they could not have been infected by *H. obsoletus* the same year. Moreover, stolbur occurred in regions where *H. obsoletus* was seldom found. Leclant and Lacote (1969), therefore, suggested that *H. obsoletus* might not be a vector of stolbur in southern France, because its adults appeared at the end of June simultaneously with stolbur symptoms in tomatoes. However, these authors did not succeed in finding another vector among the six leafhopper species tested. A similar early occurrence of stolbur-diseased potatoes was observed in Bulgaria. The stolbur agent is transmitted only rarely to potato tubers. As reported by Brcak (1958), Arabadjijev found a lot of overwintering *H. obsoletus* nymphs feeding on potato roots which may have been responsible for stolbur transmission. The importance of nymphs as vectors was thought to be neglibible because of their limited mobility in soil and their very low natural infectivity (Razvjazkina, 1950).

As stated above, there are areas in Bohemia and especially in Hungary where stolbur occurs, but *H. obsoletus* is rarely found. Thus, the discovery of new stolbur vectors was not surprising. Brčák (1954) obtained a low level of stolbur transmission using nymphs and adults of the leafhopper *Aphrodes bicincta* (Schrank). This was confirmed by Musil and Valenta (1958) and Valenta *et al.* (1960), who discovered two other new stolbur vectors among leafhoppers, *Euscelis plebeja* (Fallén) and *Macrosteles laevis* (Ribaut). Musil (1959) reported further details on stolbur transmission to various plant species by *E. plebeja*. Insufficient evidence was provided by Brčák (1954) (cf. also Blattný *et al.* 1954) concerning the vectoring ability of *Macrosteles cristata* (Ribaut). According to Posnette and Ellenberger (1963), stolbur was occasionally transmitted by *E. plebeja* and frequently by *A. bicincta* in Britain. (*H. obsoletus* has not been recorded from Great Britain).

It is uncertain whether all yellows diseases called stolbur in various contries are actually stolbur. Related but different diseases were named parastolbur (transmitted by *E. plebeja*), metastolbur (vector unknown) in Czechoslovakia (Valenta, 1961), and stolburs, C, M, SM, and P in France. It seems to me that the identity of some yellows diseases with stolbur is at least doubtful.

In Hungary, Sáringer (1961), Gáborjányi and Sáringer (1967) and Sáringer and Gáborjányi (1967) collected data on the distribution and life history of stolbur vectors *H. obsoletus, A. bicincta, E. plebeja,* and *M. laevis*. They suggested that *A. bicincta* and the very abundant species *E. plebeja* were the main vectors of stolbur in potatoes and red peppers. They also proposed chemical control of vectors in these crops. In their opinion *H. obsoletus* was only of secondary importance. However, the two leafhopper species do not occur frequently in the Roumania Plain, where *H. obsoletus* is an important vector (Ploaie, 1971). They are probably more important in the spread of clover phyllody in the Transylvania Plateau. In Czechoslovakia, Bulgaria, etc., the proposals for control of the stolbur disease are based mainly on the life history of *H. obsoletus* and suppression of sources of infection among weeds and wild plants (e.g. Valenta, 1953). In red pepper, Kovačevski (1964) obtained a better control of stolbur by closer spacing and double planting than with insecticides. Kovačevski (1958) also recommended early or late planting, barriers (e.g. by maize plants) around fields, and cover crops. Similar agronomic methods in Bulgaria, including weed control, were proposed by Kovačevski *et al.* (1964) where only *H. obsoletus* is a vector of stolbur. Martinov *et al.* (1974) obtained good results with chemical control of the stolbur disease in Bulgaria by aircraft spraying on large areas (3 to 10 ha, including protective bands 100 m wide). Applications were begun when the first *H. obsoletus* adults appeared and repeated every 5 to 7 days. In this way the incidence of stolbur was diminished from 92 or 100% to 6 or 24%, and from 90% to 10 or 12%.

Valenta (1958) investigated natural infectivity of *H. obsoletus* and concluded that it was usually lower than 10%. Experiments with *H. obsoletus* are difficult because of its high mortality under artificial conditions. Thus Valenta and Musil (1956) found that 2 hr were enough for *H. obsoletus* to inoculate the stolbur agent into plants. During her stay in Moldavia, Razvjazkina (1950) reported that

there was a 2 to 7-day latent period of the stolbur agent in *H. obsoletus* and a minimum inoculation feeding of 5 min (on leaves or stems). The natural infectivity of *H. obsoletus* reached 1.5 to 10%.

Ploaie (1968) found mycoplasma bodies of stolbur in several lobes of salivary glands of *H. obsoletus*. Giannotti *et al.* (1968e) reported finding the stolbur agent in vector hemolymph negatively stained with phosphotungstic acid. Leclant *et al.* (1971) described lesions in cells of infective *H. obsoletus*. Some cells of the posterior lobe of the salivary gland and midgut showed portions of cytoplasm rich in RNA. According to Giannotti *et al.* (1972), a mycoplasmalike agent was successfully cultivated from 3rd and 4th instar nymphs of *H. obsoletus* which apparently acted as a vector of the lavander disease. An identical mycoplasma culture was obtained which differed, however, from that obtained from clover phyllody.

Difficulty in rearing *H. obsoletus* did not permit tests of its ability to transmit other mycoplasma diseases or to obtain precise information concerning the relationship of *H. obsoletus* to stolbur. The bindweed is the main natural stolbur source and is also a host plant of *H. obsoletus*. This plant has not been investigated enough for infections with other yellows diseases as well. The stolbur agent apparently needs to be studied in further detail. Besides ordinary mycoplasma bodies in stolbur-infected plants, Cadilhac and Giannotti (1975) found helical wall-free structures in the phloem of stolbur-infected *Vinca rosea* L. These were smaller than spiroplasma, having a diameter of 30 to 33 nm, and had a dense undifferentiated inner structure. Similar rodlike particles were found associated with the stolbur mycoplasma bodies. The rodlike particles were attached to the membrane of the mycoplasma. The roles of the rods and helical structures is not known.

3.3 *Dicranotropis hamata* Boheman

In Czechoslovakia this planthopper occurs frequently on grasses, especially in humid and shady localities in July and August (Dlabola, 1954). In Poland, it is less prevalent (Nowacka, 1975). Pelov (1968) first reported the occurrence of this species in Bulgaria.

As in Scandinavia, *D. hamata* was shown by Vacke (1964b) and Vacke and Vostřák (1974) to transmit the oat sterile dwarf virus (OSDV) in Czechoslovakia. This planthopper may be an important vector of OSDV in grasslands, even in areas where it does not occur frequently.

3.4 *Javesella discolor* (Boheman)

J. discolor occurs abundantly particularly in humid and shady places in grasslands and forests and also in mountains from the end of May until the beginning of August (Dlabola, 1954). In Czechoslovakia, Vacke (1964b) and Vacke and Vostřák (1974) proved that females, males, and nymphs were able to transmit the oat sterile dwarf virus (OSDV) in a manner similar to *Javesella pellucida* (Fabricius) and *Dicranotropis hamata* Boheman. *J. discolor* is apparently not an important vector of OSDV in the field. Perhaps it may play some role in maintaining sources and spread of OSDV.

3.5 *Javesella pellucida* (Fabricius)

This holarctic species was thoroughly studied, particularly in Europe, as a vector of plant pathogens. It is the most common species in this genus. As a polyphagous feeder it lives in a wide variety of plant communities; however, humid conditions offer the best environment for its development. According to Nowacka (1975), in Poland *J. pellucida* comprises 3 to 12% of the entire hopper fauna in cereals and 1 to 18% in grasses. *J. pellucida* overwinters in nymphal stage; adults appear about the beginning of May; and maximum numbers of adults of the first generation occur at the end of May. Maximum populations of second generation adults develop at the end of July or at the beginning of August. Two generations of *J. pellucida* per year occur in Germany and France as well. In Hungary, it has two generations only under favourable weather conditions (Jászai-Virág, 1969). In cooler regions, e.g. in Britain or Scandinavia, there is only one generation of *J. pellucida* a year. In Germany, *J. pellucida* are the most abundant hoppers in orchards (Lehmann, 1973b). Harpaz *et al.* (1964/65) collected *J. pellucida* in alpine areas at 1200 to 1500 m above sea-level. The bionomics, population dynamics and enemies of *J. pellucida* were thoroughly investigated by Raatikainen (1967) in Finland. Nuorteva (1962) studied phytotoxic substances produced especially by females of *J. pellucida*. Taimr and Dlabola (1963, 1965) and Dlabola and Taimr (1965) used an autoradiographical method for field detection of labeled planthoppers which fed previously on plants supplied with $Na_2H^{32}PO_4$. The radioactive food did not cause mortality of *J. pellucida* and individuals labeled in nymphal stages retained their radioactivity until adulthood. The labeled planthoppers spread very quickly to a distance of 2 to 3 km, however, their real flight potential could not be ascertained. Taimr *et al.* (1970) proved that females and males of *J. pellucida* also fed on pine seedlings labeled with ^{32}P, but not as efficiently as in oat plants.

Rearing *J. pellucida* is easy. Supplemental artificial light is sufficient during the winter (Dlabola, 1958b). Matisová (1976) obtained primary cell cultures from *J. pellucida*; thus, perhaps, we can await utilization of tissue cultures from this plant hopper for further investigation of the respective plant pathogens.

3.5.1 The Oat Sterile Dwarf Disease

In 1954 this disease severely damaged cereals, particularly oats, in the southwest area of the hilly region of Českomoravská vysocina in Czechoslovakia. In the next two years the disease caused destruction of 70 to 100% of oats in some districts. At that time the agent of oat sterile dwarf (OSD) was obscure. Shortly, Dlabola (1957) ascertained that there was a specific relation between OSD and the planthopper *J. pellucida*. Consequently, the virus etiology of OSD was presumed by Dlabola (1958a) and Průša (1958a, 1958b). The latter proposed that the OSD agent is the oat sterile dwarf virus (OSDV) and suggested that OSDV was persistently transmitted by *J. pellucida* but not by *Laodelphax striatellus* (Fallén). Průša *et al.* (1959) presented the first experimental evidence that both adults and nymphs of *J. pellucida* transmitted the OSDV. The natural infectivity of *J. pellucida* in very damaged areas reached 86%. These authors stated the latent period of OSDV in *J. pellucida* was 3 to 4 weeks and the minimum inoculation period was half an hour. In the above paper no transovarial transmission of OSDV in *J. pellucida* was reported. However, Vacke (1966b) individually tested 3,423 nymphs (obtained from eggs of infectious females) during a 4-yr period. Only seven individuals were proven to become infectious transovarially, i.e. 0.2%. These nymphs showed their inoculativity 9 to 23 days after hatching. In Sweden, Lindsten (1974) did not obtain transovarial transmission of OSDV with *J. pellucida*.

Vacke and Průša (1962) used *J. pellucida* for the investigation of the OSDV host range. By back transmission trials they proved the susceptibility of many gramineous species, but no dicotyledon plant species was found to be susceptible. This was in disagreement with an earlier report by Heskovà *et al.* (1961); however, this has not been confirmed.

Particles of OSDV were observed in ultrathin sections of midgut cells of infectious *J. pellucida* by Brčák *et al.* (1966, 1970). Tubular structures having a diameter of about 100 nm were observed in cytoplasm contained spherical particles arranged in rows, and the centre to centre distance between virions was ca. 75 nm. Clusters of similar particles unequally stained were also detected in cytoplasm, sometimes surrounded by a membrane. However, Brčák and Králík (1969a) failed to find any virions in young tissues of OSDV infected oats. Later, Brčák and Králík (1969b) reported two possible agents of OSD found again in planthoppers: namely, virus or a mycoplasmalike agent (MLO). However, electron micrographs of bodies presumably resembling MLO did not have all the typical characteristics of MLO's. Finally, similar virus particles previously described in infective *J. pellucida* were also found by Brčák *et al.* (1972) in histoid enations caused by OSD infections (fig. 4) in oats (*Avena sativa* L.) (Fig. 5) and *Arrhenatherum elatius* (L.) Presl. The estimated diameters of outer and inner capsids were approximately 73 and 45 nm, respectively. No MLO bodies were observed in OSD diseased plants and tetracycline antibiotic failed to affect symptom development in plants or to alter the infectivity of the vector. This indicated that MLO was not involved in OSD etiology. Brčák and Králík (1973) concluded that the OSDV was apparently related to the maize rough dwarf virus.

Vacke (1964b) discovered two other planthopper vectors of OSDV in Czechoslovakia, *Javesella discolor* (Boheman) and *Dicranotropis hamata* Boheman. Males, females and nymphs of both spcies were able to transmit OSDV. All the three vector species also transmitted OSDV that causes the dwarf disease of tall oatgrass (*A. elatius*) (Vacke and Vostřák, 1974). The latent period of OSDV in all three vectors is 21 to 35 days and the planthoppers retain the inoculativity until the death. In the field, *J. pellucida* is the most important vector of OSDV. In Finland, OSDV is also transmitted by *Javesella obscurella* (Boheman).

In addition to the Scandinavian countries (Finland, Norway, Sweden) OSD was reported in Britain by Catherall (1970) who found that nearly 25% of the *J. pellucida* population caught in the vicinity of a diseased oat crop were infective. In his

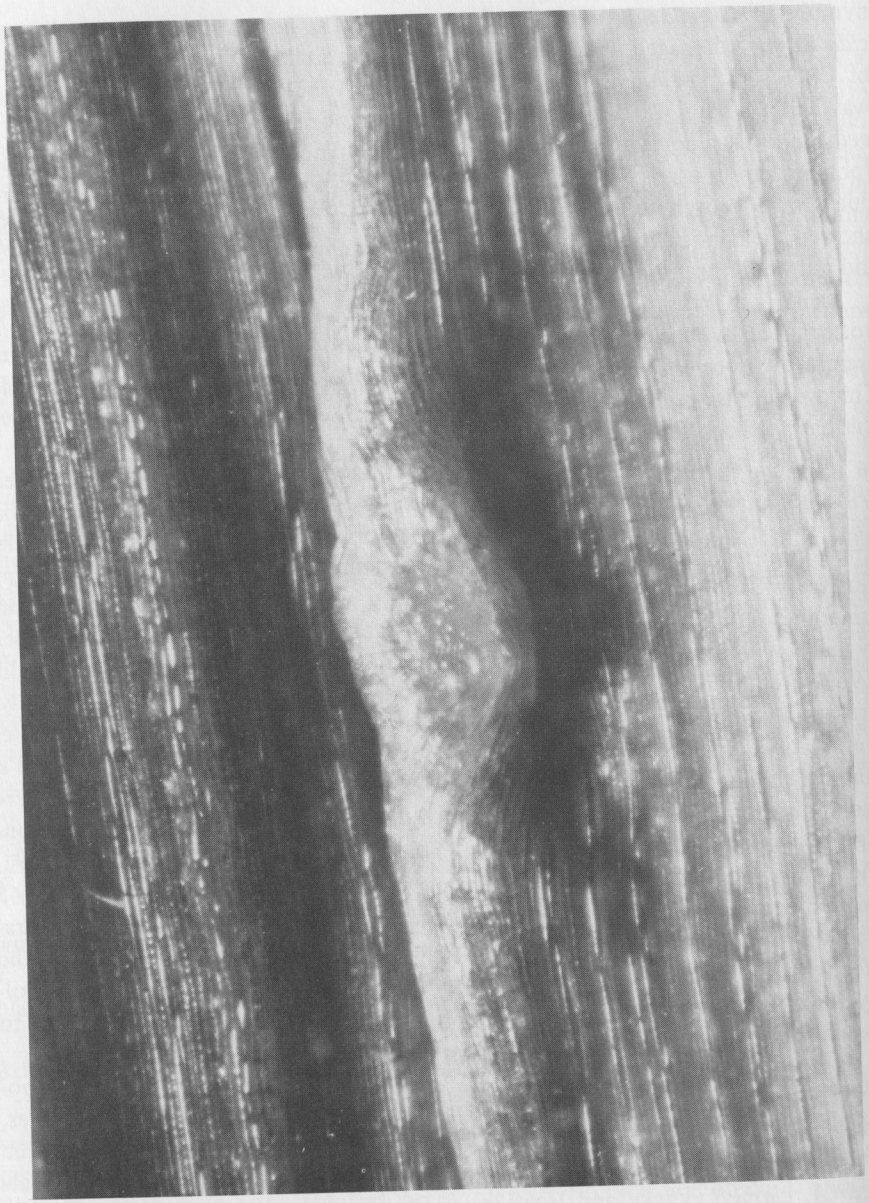


Fig. 4. A swollen vein with a histoid enation in tall oat-grass infected with the oat sterile dwarf virus (photograph by J. Brčák).

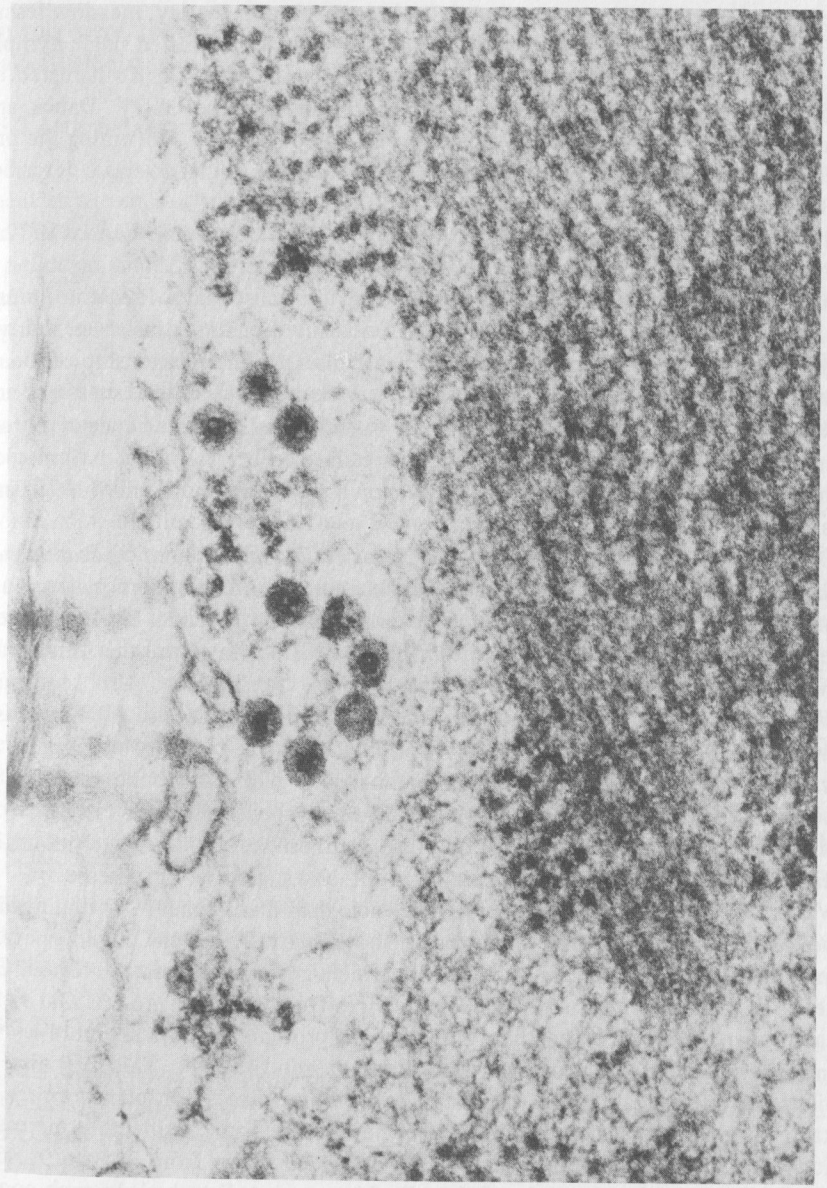


Fig. 5. Oat sterile dwarf virus particles within an enation cell of a diseased oat plant (J. Brčák and O. Králík, unpublished).

experiments, *J. pellucida* transmitted OSDV to wheat, oats, barley, meadow fescue and to ryegrasses. Plumb, Misari and Lennon (in Hirst, 1973) tested single nymphs and adults of *J. pellucida* swept from established grass swards at Rothamsted on ryegrass; 87% of nymphs and 37% of adults transmitted the OSDV. Dabek and Plumb (in Hirst, 1974) supported the virus etiology of OSD by confirming the presence of spherical particles in ultrathin sections that were similar to those described by Brčák *et al.* (1972).

In Poland, the OSDV was identified in 1970-1971 by Hoppe and Vacke (1972a), *J. pellucida* was the reported vector (Nowacka, 1975).

In the Federal Republic of Germany, Huth (1975) observed a disease in *Lolium perenne* L. and *Lolium multiflorum* Lam. that caused enations in leaves and was evidently related to OSD or maize rough dwarf disease. The relationship of the disease in *L. perenne* and OSD and MRD were demonstrated by Lesemann and Huth (1975) by electron microscopy. These particles and the occurrence of fibrous elements in viroplasm matrices in enation cells closely resembled pathological changes in plants infected with OSDV as shown by Brčák and Králík (1973) and Brčák *et al.* (1972).

OSDV is not transmissible by *Laodelphax striatellus* (Fallén) nor by *Psammotettix alienus* (Dahlbom), which indicates considerable differences from maize rough dwarf (MRD) and pupation (*zakuklivanie ovsa*) diseases (Vacke, 1964b). On the other hand maize was said to be suceptible to OSDV; however, this finding by Vacke and Průša (1962) was not verified by back transmission. Also Lindsten's (1974) comparison of characteristics of cereal tillering, OSD, and MRD diseases shows that OSDV is transmissible by *J. pellucida* and *D. hamata* but not by *L. striatellus*. Perhaps, precise serological comparisons will clarify the relations of these reolike planthopper-borne viruses of Poaceae as well as other diseases from Japan (rice black-streaked dwarf) and from southern hemisphere, such as maize wallaby ear disease (Grylls, 1975), pangola stunt, and sugarcane Fiji disease.

Vacke (1966b, 1967, 1968a) proposed ecological management for diminishing *J. pellucida* populations. Denser oat crops show relatively lower OSD infestation. In mixed cereals, *J. pellucida* prefers oats which is relatively more infested. Oat varieties also differ in natural OSDV incidences from 14.1% to 46.6%. Oat fields situated near forests or on northern slopes and in protected valleys are more severely infested with OSD than oat crops on drier or windy stands. This may also be attributable in part to more suitable overwintering places for planthoppers. A mixture of grasses and clover planted after oats resulted in considerably increased incidence of OSD during four years (from 6.4 to 69.2% or from 23.3 to 91.4%), probably because the life cycle of *J. pellucida* was not disturbed. In such conditions, planthopper populations increase and their natural infectivity increases as well. Almost all nymphs are killed by autumnal ploughing and harrowing, especially at low temperatures.

OSDV may be very destructive in cultivated grasses. For example, Vacke and Vostřák (1974) stated losses of 55 to 80% in fodder and 59 to 75% in seeds with tall oat-grass cultures, in which 60 to 65% of plants were infected. When chemical

controls were tried to prevent OSD spread, DDT aerosol gave the best results (Vacke, 1968b).

3.5.2 Arrhenatherum Blue Dwarf Virus

In the German Democratic Republic, Kempiak (1968) found the European wheat striate mosaic disease and another virus disease named *Blauverzwergung des Glatthafers* (Arrhenatherum blue dwarf virus, ABDV) transmitted by planthoppers *J. pellucida* and *J. dubia* (Kirschbaum). Mühle and Kempiak (1971) suggested that the ABDV isolated from tall oat-grass, *Arrhenatherum elatius* (L.) Presl., might be a strain of maize rough dwarf virus (MRDV), since its particles were identical with those of MRDV (or OSDV). (It should be mentioned that ABDV is unrelated to the leafhopper-borne oat blue dwarf virus from North America). They reported that ABDV had been found in Germany in 1941. This disease recurrently causes heavy damage in fodder grasses in the vicinity of Leipzig. According to Milne *et al.* (1974), ABD was observed for the first time in Bavaria and later in some districts of the German Democratic Republic.

Mühle and Kempiak (1971) ascertained that the shortest latent period of ABDV in *J. pellucida* was 14 to 16 days and that one hour was enough for acquisition the virus from an infection source. Both females and males as well as nymphs were able to transmit ABDV. Kempiak (1972b) stated that four hours were sufficient for inoculation, but longer inoculation feeding was more effective. Nymphs of *J. pellucida* carry ABDV during winter. Kempiak (1972b) also demonstrated there was poor (0.7%) transovarial transmission of ABDV in *J. pellucida*. This strongly resembles OSDV (cf. Vacke, 1966b).

It would be useful to compare experimentally ABDV and OSDV infections in some grass species, particularly since tall oat-grass proved to be a natural host of OSDV (Vacke, 1964b; Vacke and Vostrák, 1974) and because the two viruses appear to be identical (Kempiak, 1972b). In contrast to MRDV, OSDV is not transmitted by *Laodelphax striatellus* (Fallén). Thus another possibility is to re-examine the relations of ABDV to both MRDV and OSDV.

3.5.3 Dubia Disease of Barley

This disease was found to be transovarially transmitted in *Javesella pellucida* (Fabricius). Some details were reported by Kempiak (1972a, 1972b) are given in section 3.6 on *Javesella dubia* (Kirschbaum).

3.5.4 Maize Rough Dwarf Virus

Most papers on relationships of maize rough dwarf virus (MRDV) and vectors are based on experiments with *Laodelphax striatellus* Fallén). *Javesella pellucida* (Fabricius) was found to be another vector of MRDV in Italy (Harpaz *et al.*, 1964/65). The vector relationships between *J. pellucida* and MRDV were similar to these between the virus and *L. striatellus* (1-day acquisition, 15-day latent period in

planthoppers, and 1-day inoculation feeding). However, *L. striatellus* is a more efficient vector of MRDV than is *J. pellucida.*

Harpaz (1972) reported that *J. pellucida* occurs in America, whereas MRDV has not been reported there. Some authors mention the occurrence of MRDV in Czechoslovakia (Blattný and Pozděna, 1961; Blattný et al. 1965). In these papers a disease of maize resembling MRD was described and *J. pellucida* was the indicated vector. In the latter paper by Blattný *et al.* (1965), the disease was called maize rough dwarf and streak disease; however, the authors tried to find similarities of its agent to that of aster yellows. Their conclusion that the agent of the maize disease was a strain of aster yellows is based on insufficient data. The maize disease agent was reported to be transmitted by the planthopper, *J. pellucida* and presumably by three additional leafhopper species from yellows-infected *Origanum vulgare* L., *Anagallis arvensis* L., and *Zea mays* L. Although a vein thickening was an important symptom, especially in field maize plants, there was some confusion because phytotoxemia resulting in vein hypertrophies also occurred in their experiments. Similar effects of hoppers' saliva in maize laeaves were reported elsewhere (cf. Maramorosch, 1959; Maramorosch *et al.*, 1961; Harpaz, 1972). In one case, Grylls (1975) provided evidence that the maize wallaby ear disease in Australia was caused by a MRDV related virus and not by insect salivary toxins. Blattný *et al.* (1965) reported finding this disease from many localities in Czechoslovakia. Nevertheless, no one has continued the study of this maize disease in Czechoslovakia, therefore a definite identity with MRDV remained obscure.

3.5.5 European Wheat Striate Mosaic

Wheat striate mosaic diseases transmitted by *Javesella pellucida* (Fabricius) were independently investigated in Great Britain and Czechoslovakia. Hitherto, identity of both disease has not been proved experimentally.

In 1956, the European wheat straite mosaic (EWSM) transmitted by *J. pellucida* was ascertained in England (Bawden, 1957). Slykhuis and Watson (1958) stated that EWSM agent was transmitted efficiently (by 88 percent) through eggs of infectious females of *M. pellucida* to progeny. Some females did not show inoculativity, but their progeny did so. Watson and Sinha (1959) discovered lines of *J. pellucida* showing different transmission efficiency, and that was correlated with more or less efficient transovarial transmission of EWSM agent. In some cases, no transovarial transmission was ascertained. Only females that acquired EWSM in nymphal stage showed transovarial transmission. Later, Sinha (1960) found that only one female out of 20 that acquired EWSMV as adults transmitted it to its progeny. *J. pellucida* females that acquired EWSM agent from infected plants during mating did not produce infective progeny, although the adults themselves transmitted EWSM. This phenomenon suggested that the development of ovaria influenced transovarial transmission rather than the amount of infective doses in the planthopper.

It was observed that *J. pellucida* females that fed on infected plants in nymphal stage produced 40% fewer progeny than EWSM-free females. Death of some embryos infected with the EWSM agent was observed, which indicated pathogenicity of EWSM for its vector. Sinha (1960) demonstrated that nymphs of *J. pellucida* were more efficient vectors than adults and that this phenomenon occurred because the EWSM agent passed through the gut wall of nymphs more efficiently. Adult *J. pellucida* with punctured abdomens (but not those punctured into the thorax) just before or shortly after the acquisition feeding, showed increased ability to transmit EWSM, whereas punctures performed a week later did not effect the inoculativity.

The cause of the embryonic mortality of *J. pellucida* eggs infected with EWSM agent was investigated by Kisimoto (in Gregory, 1961) who concluded that the involvement of EWSM agent was doubtful since inbreeding developed similar abnormalities in planthoppers that were free from the agent. Brother-to-sister matings produced females whose eggs (31%) were abnormal and failed to hatch. Further inbreeding caused 48% abnormality in the F2 generation, compared with only 3% abnormality in outbred F2 females. A similar situation was reported by Kisimoto and Watson (1965) who worked with *J. pellucida* and *Javesella dubia* (Kirschbaum), another vector of EWSM. Also, some individuals in the second generation of *J. pellucida* that hatched produced sterile females. Thus, the cause of embryonic mortality was apparently due to inbreeding rather than EWSM infection. Raatikainen (1967) presented additional factors that together with parasites and predators reduced the progeny of *J. pellucida* in the egg stage; on the average only 37% survive to eclosion and one female lays an average of 402 eggs.

Ammar (1975a) thoroughly investigated the effect of EWSM acquired by feeding on diseased plants on the biology of different lines of the planthopper vectors *J. pellucida* and *J. dubia*. Ten lines of *J. pellucida* transmitted EWSM with an average efficiency of 31% compared to 10% efficiency for eleven lines of *J. dubia*. No significant variation was found between infective and non-infective planthoppers in survival of nymphs to adulthood, adult longevity of either sex, total and rate of egg production per female, or survival of eggs to eclosion. Transovarial transmission of EWSM occurred in 6 to 43%. With progenies of *J. pellucida* that acquired EWSM transovarially, Ammar (1975b) found, that the proportion of infective nymphs ranged from 85 to 96%. EWSM had no effect on the viability of eggs, however, mild pathogenic effects on *J. pellucida* were induced in nymphal and adult stages. EWSM acquired transovarially for two generations decreased the longevity of adults by 14%. Certain lines of *J. pellucida* seemed to be more susceptible than others to the adverse effects of inherited EWSM agent. Ammar (1975b) also confirmed that inbreeding decreased the viability of eggs of *J. pellucida*. Furthermore, inbreeding for two generations resulted in a 40% increase in mortality of nymphs and more than 50% reduction in the longevity of adults.

According to Slykhuis and Watson (1958), there was a latent period of at least 8 days of the EWSM agent in *J. pellucida* when it was acquired from diseased plants. The same interval at 20 to 25°C was reported by Serjeant (1967) with *J. pellucida* injected (at 5°C) with extracts from infective planthoppers or plants. In his first communication, Serjeant (in Gregory, 1961) reported a latent period

of 10-23 days for EWSM agent in *J. pellucida* when planthoppers were injected with plant extracts diluted 1:2; higher dilutions did not render the planthoppers infective. Serjeant (1967) indicated that better results could be achieved if the EWSM agent was obtained from hoppers rather than from plants. EWSM agent from planthoppers was still infectious after 10 min. at 30°C, or 36 h at 5°C, and could be stored for several months at -15°C.

Many authors anticipated the virus etiology of EWSM disease. Serjeant (1967) failed to detect specific particles by means of electron microscopy. Ammar *et al.* (1970) observed viruslike particles (65 x 30 nm) in the cytoplasm of some cells in the salivary glands, gut wall, and brain of *J. pellucida* that were apparently unassociated with EWSM. Thus, the EWSM agent has not been found.

Diseases very similar or identical to the EWSM were found in England, Germany, Spain, and perhaps Denmark, Poland and Roumania. Apparently the same disease agent occurring in Finland and Sweden can be transmitted by *Javesella obscurella* (Boheman).

In Czechoslovakia, Průša *et al.* (1959) reported a disease closely related to EWSM called wheat-striate mosaic (WSM), that had the same vector, *J. pellucida*, and that was efficiently transovarially transmissible. Průša (1960a, 1960b) suggested that it might be identical to EWSM. He ascertained that WSM was transmitted both by adults of both sexes and nymphs of *J. pellucida* and that there were efficient and inefficient lines of the vector. Some individual *J. pellucida* were shown to transmit simultaneously the WSM agent and the oat sterile dwarf virus (OSDV). A group of females, 24.4% of which were infective produced progenies of 14.9% infective nymphs (that acquired the WSM agent transovarially). After 26 to 34 days the infectivity of the group increased by 61.6% and after 40 to 50 days by 98.2%. Under field conditions, a population of *J. pellucida* contained only 14.4% of noninfected individuals; 1.9% carried WSM, 61.2% OSDV, and 22.5% transmitted OSDV and sometimes simultaneously WSM (Průša and Vacke, 1960a, 1960b). While 30 min were enough for infective *J. pellucida* to inoculate OSDV into plants, 9 hr were necessary with WSM.

The host range of WSM includes at least 18 species of Poaceae (Vacke and Průša, 1961). Using nymphs of the second and third instars Vacke (1975) checked some supposed natural hosts of WSM; *Bromus commutatus* Schrad., *B. secalinus* L., *Lolium temulentum* L., *Secale cereale* L., and *Poa annua* L. were shown to carry the WSM agent. Also, Watson (in Gregory, 1961) demonstrated natural infection of *Poa annua* with EWSM.

A comprehensive review on WSM was published by Průša (1965), including a comparison of WSM with similar diseases, the economic importance of WSM, its epiphytology, and proposals for simple control measures.

In the German Democratic Republic, Kempiak (1968, 1972b) proved the occurrence of a disease that was apparently identical to the EWSM. The transovarial transmission in *J. pellucida* was 22 to 86% (65% on the average). The latent period of the agent in the vector was 24 days or less. An inoculation period of 4 hr was sufficient for transmission, but more effective transmission was achieved with

longer inoculation access periods. Bremer and Raatikainen (1975) reported the occurrence of a EWSM-like disease in West Turkey. This disease was transmitted by an unidentified planthopper, presumably by *J. pellucida.*

3.5.6 Diseases with Presumptive Yellows Etiology

Blattný (1957, 1958, 1959) concluded that *J. pellucida* was able to transmit yellows-type (mycoplasma) diseases. In his papers, transmission of a yellows disease of *Anagallis arvensis* L. and the so called pseudoclassic stolbur with the leafhopper *Macrosteles laevis* (Ribaut) and the planthopper *J. pellucida* were reported. Like pseudoclassic stolbur, such yellows diseases were reported in localities where the "classic" stolbur vector *Hyalesthes obsoletus* Signoret was absent. It involved, e.g., *Convolvulus arvensis* L., *Anagallis arvensis* L., and *Stellaria media* (L.) Vill. Attempts to transmit the agent of "pseudoclassic" stolbur using the two hopper species, dodder (*Cuscuta campestris* Yunck.), or grafting to tomato and potato plants did not result in characteristic symptoms of stolbur disease. However, Blattný observed and described quite new symptoms in those test plants, and adjudged them to the imaginary "pseudoclassic" stolbur. Hitherto, these results have not been reexamined. To my opinion, some of the yellows diseases in question, especially in *Stellaria media*, might be caused by clover dwarf, or by other mycoplasma agents with *Anagallis arvensis.*

Blattný *et al.* (1970) investigated the origin of alterations in pine tree (*Pinus silvestris* L.) seedlings that resembled witches' broom diseases. They reported that in some instances these alterations were presumably caused by a virus or by a mycoplasmalike agent and that they were transmitted by both *J. pellucida* and *M. laevis.* The two hopper species were said to be able to transmit the pine witches' broom agent to *Stellaria media.* Since the authors suggested other causes that induced identical alterations in pine, it will be hardly possible either to confirm or to deny their results.

3.6 *Javesella dubia* (Kirschbaum)

This species usually occurs as a common and frequent planthopper both in lowlands and mountains, as well as in grasslands, clearings, and grassy shady forest localities (Dlabola, 1954).

In England, Kisimoto (in Gregory, 1961) identified *J. dubia* and *Javesella pellucida* (Fabricius) as vectors of European wheat striate mosaic (EWSM) disease. *J. dubia* showed abnormalities in embryonic development similar to those in *J. pellucida* that were apparently caused by inbreeding (Kisimoto and Watson, 1965). Ammar (1975a) showed that several lines of *J. dubia* transmitted EWSM less efficiently (10%) than *J. pellucida* (31%).

Kempiak (1968) reported that *J. dubia* and *J. pellucida* were vectors of Arrhenatherum blue dwarf virus.

3.6.1 Dubia Disease of Barley

According to Kempiak (1972a, 1972b) another disease of gramineous plants other than Arrhenatherum blue dwarf virus (ABDV) and European wheat striate mosaic (EWSM), namely the Dubia disease of barley (DDB), is transmitted also by *Javesella pellucida* (Fabricius) and occurs in the German Democratic Republic. Like the oat pseudorosette disease (*zakuklivanie ovsa*) described from the U.S.S.R., DDB is characterized by the presence of big twisted inclusions in cells of infected plants. The agent of DDB was isolated from *J. dubia* and was transovarially transmissible in more than 50% of females of *J. pellucida*. DDB could be transmitted (like ABDV or EWSM) to oats, wheat and barley. Kempiak (1972a) suggests possible relations of DDB to the following diseases: northern cereal mosaic, rice stripe, Phleum green stripe disease (from Scandinavia), and barley yellow striate mosaic (from Italy). A relationship of this disease to the oat pseudorosette (pupation disease, *zakuklivanie ovsa*) may be doubtful.

3.7 *Laodelphax striatellus* (Fallén)

This palearctic planthopper species, formerly named *Calligypona marginata* (Fabricius), is also widely distributed in Siberia and some areas in the tropics. More details on its bionomics were presented by Harpaz (1972). In northern countries (e.g. Sweden), *L. striatellus* has a single generation each year. Six generations were reported in Southern Kyushu in Japan. In Bulgaria, *L. striatellus* was first reported by Dirimanov and Charizanov (1965). Charizanov (1972) found four generations a year from the beginning of April until the middle of October. *L. striatellus* overwinters in Bulgaria as a second nymphal instar. Third or fourth instars were reported to overwinter in the U.S.S.R. (Klinkowski and Kreutzberg, 1958). Males in individual generations live 16, 21, 31, and 41 days, females, 22, 28, 42, and 49 days on the average. One female produces 83 to 96 eggs that hatch in four generations after 6 to 16, 7 to 18, 5 to 21, and 14 to 24 days. The nymphal stages last 16 to 21, 17 to 25, 18 to 26, and 154 to 189 days with overwintering nymphs. In northern Italy, Conti (1972) found two generations of *L. striatellus* each year. A similar observation was reported by Jászai-Virág (1969) from Hungary, where this widely distributed planthopper is more abundant than *Javesella pellucida* (Fabricius). For these population studies, light traps were used (cf. Virág, 1967). In Poland, *L. striatellus* is less frequent than *J. pellucida* (Nowacka, 1975). In Czechoslovakia, *L. striatellus* occurs very frequently in grasslands, steppes, swamp vegetation, bushes, and even in mountains (Dlabola, 1954). Specific relationships of *L. striatellus* to some plant disease agents may contribute to their differentiation. For example, maize rough dwarf virus is transmitted both by *L. striatellus* (being its main known natural vector) and *J. pellucida* (Harpaz *et al.*, 1964/65), whereas the related oat sterile dwarf virus is transmitted by *J. pellucida* but not by *L. striatellus* (Vacke, 1964b; Lindsten, 1974).

3.7.1 Maize Rough Dwarf Virus

The monograph by Harpaz (1972) contains very detailed information. The maize rough dwarf disease (MRDV) was described first in Italy as *"nanismo ruvido del mais"* in 1949. Its virus origin was demonstrated in 1959 in Israel and the vector *L. striatellus* was discovered in 1961. In Europe MRDV was reported from Italy, Spain, France, and southern Switzerland. Lovisolo (1971) includes Yugoslavia in his chart. References from Czechoslovakia and Germany are unreliable. Of course, there are many countries (e.g. Great Britain) where *L. striatellus* occurs, but MRDV does not. In Israel, additional vectors of MRDV were described, namely *Delphacodes propinqua* (Fieber) and *Sogatella vibix* (Haupt). The planthopper *D. propinqua* is known to occur in also Bulgaria (Dirimanov and Charizanov, 1965; Pelov, 1968) and is infrequently found in the southern region of Czechoslovakia (Dlabola, 1954).

MRDV particles are easily detectable in veinal hyperplasia (enations) caused by an abnormal proliferation of phloem elements in infected plants. The same particles were found in inoculative *L. striatellus* by Vidano and Bassi (1966). Gerola *et al.* (1966) observed tubular structures containing MRDV particles in vein swellings of maize leaves and identical virus particles in a crystal-like arrangement in the fat body of the vector *L. striatellus*. Vidano (1967, 1969, 1970) thoroughly described the systemic infection of *L. striatellus* with MRDV. He suggested the fibrillar viroplasm (occurring e.g. in mycetomes) to represent the main site of MRDV reproduction. In such sites he found incomplete MRDV particles in which the inner core was poorly osmiophilic. In the midgut, epithelial cells contained conspicuous phagocytic vesicles and groups of bacilliform cores. The phagocytic vesicles looked like electron-dense inclusions with a lysosomelike structure. Gut and salivary glands were found to be infected most frequently; nevertheless, an extensive systemic infection of the planthopper was ascertained by the presence of MRDV particles in hemocytes, hypodermis, muscles, tracheoblast, brain, and ovarioles. Electron micrographs illustrated phases of MRDV morphogenesis. The results by Vidano published in many papers were thoroughly summarized by Harpaz (1972), who concluded that MRDV was primarily an insect pathogen.

Harpaz *et al.* (1964/65) demonstrated a 1-day minimum acquisition feeding period for *L. striatellus*, a minimum latent period of 15 days, and an inoculation feeding of 5 hr. Conti (1974) reported some more precise data: He obtained the shortest latent period of 10 days (8 days for planthoppers after injection). After a 2-day acquisition feeding period, the vectors showed a longer latent period, at least 14 days. The highest transmissibility was obtained after a 24-day incubation period with planthoppers given an acquisition access period of 5 to 10 days. The planthoppers fed for 2, 5, or 10 days on infected plants were able to transmit MRDV at levels of 25, 35, or 39% respectively. The 4th-instar nymphs transmitted MRDV with 46% efficiency, the 2nd-instar nymphs 40%, and adults 20%. According to reports from Israel, transovarial transmission of MRDV seems to occur only rarely (cf. Lovisolo, 1971).

MRDV was partially purified for the first time by Lovisolo *et al.* (1967) from infected maize roots. Wetter *et al.* (1969) succeeded in purifying MRDV both from plants and vectors. In their serological investigation, no specific reaction between MRDV and wound tumor virus antiserum was obtained, which indicated that the two viruses were unrelated. Lovisolo (1971) reported serological relationships between MRDV and rice black-streaked dwarf virus, another member of the plant reoviruslike group.

Milne *et al.* (1973) used *L. striatellus* to determine the infectivity of partially purified MRDV particles. He concluded that only complete virus particles were infectious, as demonstrated by injecting virus-free planthoppers with various fractions. Planthoppers showed inoculativity 8 days after they had been injected.

In Italy, MRDV had been known only in maize, until Luisoni and Conti (1970) discovered a new natural host, *Digitaria sanguinalis* (L.) Scop. Although this plant is not a perennial grass, it may represent an important source of infection, since it is a widely spread weed in maize crops and is preferred by *L. striatellus* for feeding and laying eggs. *L. striatellus* does not breed on maize in the field and only occasionally visits maize plants during migrations (Lovisolo, 1971). Adults of *L. striatellus* survive only few days on maize when reared experimentally. However, *L. striatellus* acts as principal vector of MRDV in Italy, where its dispersal coincides with sowing of maize. Another natural host of MRDV was ascertained by Conti (1972b), who found MRDV infected *Echinochloa crus-galli* (L.) P.B. plants. This annual species was formerly known as an experimental host only. MRDV overwinters in nymphs of *L. striatellus* as demonstrated by Conti (1972b), who recovered MRDV from overwintering nymphs at the beginning and at the end of the diapause period. This was an important contribution to the epidemiology and control of MRDV. Reviewing Italian experiences (e.g. of professor Grancici) Lovisolo (1971) and Conti (1972b) proposed some control measures to minimize MRDV spread: insecticide sprays should be applied to weedy grass borders surrounding the fields about 20 to 30 days before the sowing of maize, or insecticides should by applied siumltaneously with weed control before the appearance of winged forms of *L. striatellus* in early April. Delayed sowing of maize, which could be recommended in Israel was not generally applicable in Italy. Some control of MRDV might also be obtained by employing several maize hybrids of different susceptibility to MRDV.

3.7.2 Barley Yellow Striate Mosaic Virus

The barley yellow striate mosaic virus (BYSMV) was isolated by Conti (1969a) from *L. stritellus* planthoppers collected in the field in northern Italy. Those planthoppers transmitted BYSMV to oats, wheat and barley, but not to maize. Bacilliform particles of BYSMV resemble some other plant viruses, e.g. winter wheat mosaic virus from the U.S.S.R. Nevertheless, Conti (1969b) claims that BYSMV differs from any hitherto described virus.

The minimum latent period of BYSMV in the planthopper is 8 to 10 days and the 3-days acquisition access period is enough for obtaining infective planthoppers.

Suspensions of partially purified BYSMV prepared from barley and injected into virus-free *L. striatellus* rendered them infective; the infectivity of planthoppers ranged from 15 to 43% and individuals were able to transmit BYSMV in 4 or 6 days after injection. Planthoppers, once infective, continued to transmit the virus for life (Conti, 1969b).

Conti (1972a) succeeded in isolating BYSMV from self-setting wheat plants grown from occasionally dispersed seeds. A successful transmission of partially purified virus (from plants) by injecting planthoppers was reported. However, the latent period of the virus in insects ranged from 14 to 21 days. Summarizing his results dealing with minimum efficient periods of the transmission process, Conti (1974) characterized the relationship between *L. striatellus* and BYSMV as follows: acquisition, 5 hr; latent period, 10 days (or 6 days after injection); inoculation, 15 min. This suggested that BYSMV was more easily acquired and transmitted by *L. striatellus* than the maize rough dwarf virus.

Thus, BYSMV belongs to propagative planthopper-borne rhabdoviruses infecting gramineous plants. Bacilliform particles (330 x 45 nm) were observed by Appiano and Conti (1973) and Conti and Appiano (1973) in ultrathin sections of BYSMV infected barley cells. The latter paper offers further cytological details on infection process in barley.

The economic importance of BYSMV seems to be negligible in northwest Italy, where the virus has been discovered. Conti (1974) mentioned that a virus of wheat closely resembling BYSMV was found in southern France; Leclant and Signoret (1974) reported a rhabdovirus in wheat transmitted by *L. striatellus* as well.

3.7.3 Note

Hitherto, no extensive experimental comparison of planthopper-borne agents has been made, although individual attempts were started, particularly with the reolike viruses infecting gramineous plants. For example, Lindsten (1974) compared characteristics of oat sterile dwarf (OSD), maize rough dwarf (MRD) and cereal tillering disease (CTD), Lovisolo *et al.* (1974) discussed seven diseases of gramineous plants in the world known to be caused by reolike viruses: namely, Arrhenatherum blue dwarf, CTD, MRD, OSD, Pangola stunt, rice black-streaked dwarf and sugarcane Fiji disease. Also the maize wallaby ear disease from Australia apparently belongs to this group, as shown by Grylls (1975). Milne *et al.* (1975) proved that particles of OSDV, CTDV, MRDV, and ABDV are morphologically indistinguishable from each other (or structurally very similar). Some of the viruses mentioned were compared serologically and certain evidence of their relationships was obtained.

Until now, no results of comparative experiments have been published which could elucidate the relations of well known cereal diseases described particularly from the U.S.S.R. to other diseases. For example, the oat pseudorosette (or pupation) disease (*zakuklivanie ovsa*) was reported to be transmitted by *L. striatellus* by Suchov and Vovk just in 1938. Thus, a lot of further work in this field is expected.

3.8 *Philaenus spumarius*(Linné)

P. spumarius is a polyphagous and very abundant froghopper in Europe, Asia, Japan and North America. In Europe many authors made unsuccessful attempts to prove its ability to transmit some viruses and mycoplasmas. *P. spumarius* is known to be a vector of plant pathogenic agents in Nearctic regions, but in the Old World, Harpaz (1964) reported it to be a vector of the Ballota split leaf disease in England. Single nymphs of this froghopper were used in his experiments. However, this result has not been confirmed by further experiments and there are no references on the etiology and properties of this disease of *Ballota nigra* L.

It is worth noting that Vago and Flandre (1963) reported the first successful cultivation of hopper cells obtained from gonads, gut and hypodermis of *P. spumarius.*

3.9 *Macropsis scotti* Edwards

The Scott's leafhopper was shown to be a vector of Rubus stunt disease (mycoplasma) in Great Britain by Legg (in Cadman, 1961). Nielson (1968) calls attention to the fact that this species is difficult to distinguish from the closely related species *Macropsis fuscula* (Zetterstedt), another vector of Rubus stunt mycoplasma.

3.10 *Macropsis fuscula* (Zetterstedt)

In 1951, de Fluiter and van der Meer (1953) in the Netherlands began experiments with Rubus stunt disease (RSD) and reported that it could be transmitted by the European raspberry leafhopper, *M. fuscula.* Thereafter, de Fluiter and van der Meer (1955) demonstrated that *M. fuscula* transmitted RSD persistently.

The distribution of *M. fuscula* was reported by Nielson (1968). In Czechoslovakia, *M. fuscula* is not a very common leafhopper (Dlabola, 1954). The RSD also occurs in Czechoslovakia, Latvian S.S.R., Denmark, Norway, Sweden, Great Britain, France, and, according to Richter (1963), also in both German republics and Bulgaria. Blattný (1959) reports that it occurs north of Caucasus.

The mycoplasma etiology of RSD was proved by Murant and Roberts (1971) by means of electron microscopy and effects of aureomycine on infected blackberry, loganberry and raspberry.

M. fuscula passes the winter in the egg stage on bark of young canes of raspberry, blackberry and wild *Rubus* species. It produces only one generation a year. Adults occur on Rubus plants from July to September (de Fluiter and van der Meer, 1953). From their observations and experiments, de Fluiter and van der Meer (1955) were inclined to believe, that there were two lines (strains) of *M. fuscula*, one living on raspberry and the other on blackberry. In this paper a control of RSD was proposed based on killing eggs and nymphs of the vector. Complete instructions for control of all stages of the vector were presented by de Fluiter and van der Meer (1958). Finally, van der Meer and de Fluiter (1962) reported that populations of *M. fuscula* living on various Rubus species usually do not migrate to other *Rubus* species grown under different ecological conditions. This might

clarify why wild blackberry plants did not act as important infection sources for cultural raspberries. Consequently, in the Netherlands, there were some localities with abundant RSD-infected blackberries, but cultivated raspberries were not infected.

3.10.1 Note

In German Democratic Republic, Lehmann (1973a) isolated a yellows agent from *Rubus* sp. which was transmitted by *Euscelis plebeja* (Fallén) and produced clover phyllody symptoms in *Trifolium repens* L. and *Chrysanthemum carinatum* Schousb.

3.11 *Aphrodes albifrons* (Linné)

According to Evenhuis (1958b), this leafhopper species was able to transmit the clover phyllody agent in the Netherlands.

3.12 *Aphrodes bicincta* (Schrank)

This holarctic species occurs commonly in many kinds of vegetation. Usually, it is prevalent in grasslands, fields (especially on clover and alfalfa), and also in paludinous localities, dry steppes and hillsides (Dlabola, 1954). It is a polyphagous feeder having only one generation a year and overwintering in the egg stage.

Adults and nymphs of *A. bicincta* were shown to transmit the stolbur agent with a low efficiency (Brčák, 1954). This was confirmed in Czechoslovakia by Musil and Valenta (1958), Valenta *et al.* (1960), Valenta (1961) and in Great Britain by Posnette and Ellenberger (1963). However, Kuroli (1972a) in Hungary and Kovačevski *et al.* (1964) in Bulgaria failed to obtain stolbur transmission using *A. bicincta.*

In Germany Heinze and Kunze (1955) succeeded in transmitting yellows agent to aster and *Vinca rosea* L. plants with *A. bicinta.* In aster plants symptoms differed from those that developed following transmission of a yellows agent by *Macrosteles laevis* (Ribaut); they were not sure if the same agent was involved.

Clover phyllody (CP)-like agents were found to be transmitted by *A. bicincta* in Switzerland (Bovey, 1957) and in the Netherlands (Evenhuis, 1958a). Musil and Valenta (1958) demonstrated transmission of CP by *A. bicincta* in Czechoslovakia. Afterwards, this was confirmed in the U.S.S.R. by Razvjazkina (1962). In her experiments, 80 to 90% of nymphs transmitted CP in contrast to low transmission efficiency of adults. CP agent transmission by *A. bicincta* was also reported in Hungary by Kuroli (1972a) and in Italy by Belli *et al.* (1972). It is likely that the same CP transmitted by *A. bicincta* in Europe also occurs in Canada (Chiykowski, 1962). *A. bicincta* was found to be an efficient vector of CP (strawberry green petal) in England by Posnette and Ellenberger (1963). They failed to obtain transmission of clover witches' broom and Delphinium yellows with *A. bicincta.*

In France, Cousin (1968) showed that *A. bicincta* transmitted CP and the clover dwarf (CD) as well. Musil (1960) investigated the natural infectivity of *A. bicincta* from a white clover field severely infested with CD and concluded that only 2 to 5% of leafhoppers carried the CD agent. He also stated that the latent period of CD (and similary of stolbur and CP) in *A. bicincta* varied from 14 to 76 days. Valenta and Musil (1963) proved that *A. bicincta* also transmitted the parastolbur agent.

Harpaz (1964) reported that, in one case, the Ballota split leaf disease agent was transmitted by *A. bicincta* from *Lamium album* L. to *Ballota nigra* L. (The etiology of this disease is not known).

Staniulis and Genyte (1976) obtained transmission using *A. bicincta* with some (not otherwise identified) yellows diseases of mycoplasma origin in *Cirsium oleraceum* Scop., *Matricaria inodorata* L. and *Plantago media* L. to clover in Lithuania S.S.R.

Giannotti (1969b) investigated *A. bicincta* more thoroughly. In CP agent-carrying leafhoppers, he observed mycoplasma bodies and cellular lesions in some tissues. As with *Euscelidius variegatus* (Kirschbaum), granulous or amorphous cytoplasmic materials containing DNA, RNA, and proteins were detected in infective leafhoppers.

The vector capabilities of *A. bicincta* were thoroughly discussed. Posnette and Ellenberger (1963) incriminated this species as probably chiefly responsible for transmission of the green petal disease agent in strawberry crops. Whereas *Euscelis* and *Macrosteles* spp. seemed to be the principal vectors under dry conditions, *A. bicincta* was more abundant in damp situations, such as provided by dense vegetation; consequently, irrigated strawberry fields were severely infested. In the wet southwest region of Wales in strawberries there was a higher incidence of green petal disease than in east of England, where CP was more prevalent in clover. These conclusions were in agreement with a report by Frazier and Posnette (1957) who found an unusually severe (up to 30%) infestation of strawberries with CP in Sussex in 1956 after a dry autumn in 1955. The part of the field watered in August and September showed twice the infestation of the part which had not been watered. The authors clarified this phenomenon by moving of *A. bicincta* from various plants suffering from drought in the vicinity.

Săvulescu and Ploaie (1964, 1967) estimated that *A. bicincta* was less active and less widely distributed than *Euscelis plebeja* (Fallén) in Roumania. *A. bicincta* occurs rarely in Roumania Plain, but it is more abundant in the Transylvania Plateau (like *E. plebeja*), where CP occurs frequently. Also in France Cousin (1968) and Moreau *et al.* (1968) found *A. bicincta* to be a less important natural vector than *E. plebeja*. *A. bicincta* has only one generation a year and overwinters in the egg stage. On the other hand, it is a fully polyphagous feeder and its individuals live for a very long time, which enables them to infect many plants.

The distribution and life history of *A. bicincta* in Hungary were published by Sáringer (1961). Kuroli (1972a) suggested this abundant leafhopper was important in transmission of stolbur disease, particularly in the circulation of the stolbur agent among weed hosts. Consequently, some investigation of vector control in Hungary also concerned the use of insecticides for control of *A. bicincta* (Gáborjányi and Sáringer, 1967) and even possible applications of some alkyl-aryl-ethers showing antifeeding, antioviposition, and repellent effects on *A. bicincta* and *E. plebeja* (Matolcsy *et al.*, 1968).

3.13 *Macrosteles viridigriseus* (Edwards)

In Britain, Frazier and Posnette (1956, 1957) reported that *M. viridigriseus* was an efficient vector of clover phyllody (CP, green petal of strawberry) and witches' broom. However, like *Euscelis lineolata* Brullé, it failed to transmit this agent to strawberry plants. Harpaz (1964) determined that *M. viridigriseus* leafhoppers collected outdoors in England carried the CP agent.

3.14 *Macrosteles cirstata* (Ribaut)

Brčák (1954) tried to transmit the stolbur disease agent using *M. cristata*, but evidence for transmission of any pathogen was inconclusive. Therefore, this species cannot be considered a vector of stolbur. These inconclusive results were reviewed in a paper by Blattný *et al.* (1954) and cited erroneously in several other reviews. However, this leafhopper species has been shown to be a vector of some yellows diseases. Evenhuis (1958b) reported that *M. cristata* was a vector of clover phyllody in the Netherlands. In Germany, Lehmann (1973a) proved that *M. cristata* transmitted yellows agents from *Godetia grandiflora* Lind., *Primula denticulata* Smith, and cauliflower to *Chrysanthemum carinatum* Schousb. which developed symptoms of clover dwarf.

M. cristata was also chosen by Proeseler and Eisbein (1974) as a model insect for attempting amputation of stylets by three different methods.

3.15 *Macrosteles quadripunctulatus* (Kirschbaum)

Suchov and Vovk (1945) reported for the first time that *M. quadripunctulatus* was a vector of *kok-saghyz* yellows in the U. S. S. R. In some countries, e.g. in Czechoslovakia, this species is rare and has not been studied as a vector. Ploaie (1969b, 1971) obtained transmissions of a mycoplasma agent by this leafhopper that was similar to Californian aster yellows in Roumania. In Italy the Tagetes witches' broom, caused by mycoplasma, was found to be transmitted by *M. quadripunctulatus* (Belli *et al.*, 1972).

Marchoux *et al.* (1972) ascertained that *M. quadripunctulatus* was a vector of carrot proliferation disease in southwest of France. This was confirmed by Leclant *et al.* (1974) who simultaneously provided evidence of transmission by the psylla *Trioza nigricornis* Forst. of an apparently different agent of carrot proliferation. Difference between the two agents were detected in infected *Vinca rosea* L. plants, but not in carrot plants. It is worth noting papers by Giannotti and Vago (1974) and Giannotti *et al.* (1974) who described the presence of both mycoplasma bodies and rickettsialike bacteria in dwarfed and proliferated carrot (*Daucus*

carota L.) and in the psylla vector *T. nigricornis*. This indicated that a mixed infection was probably responsible for the disease. The disease might be also compared with parastolbur infection in carrot transmitted by *Euscelis plebeja* (Fallén) as shown by Musil (1964a).

3.16 *Macrosteles laevis* (Ribaut)

M. laevis is a palearctic species and usually one of the most common leafhoppers, especially prevalent on gramineous plants. It is a polyphagous species that may also feed on pine, *Pinus silvestrix* L., as shown by Taimer *et al.* (1970) who fed leafhoppers on pine seedlings labeled with ^{32}P. There are two generations of *M. laevis* each year in Czechoslovakia, Hungary (Gáborjányi and Sáringer, 1967) and Poland (Nowacka, 1975). In Poland, *M. laevis* occurs from the middle of May on till the end of September and sometimes until October. The first generation reaches its maximum in the second half of June, the second generation in August until mid September. *M. laevis, Psammotettix alienus* (Dahlbom), and *Javesella pellucida* (Fabricius) represent a regular component of insect fauna particularly on grasses, cereals, fodder leguminous plants, umbelliferous and medicinal plants in Poland (Nowacka, 1975). In Bulgaria, Charizanov (1970) reported three generations of *M. laevis* a year beginning at the end of April, June, and July, respectively. The average life span of females and males, the average number of eggs, egg time, and nymphal time of the first generation reach 22 and 17 days , 48, 12 to 18 days and 19 to 34 days, respectively; for the second generation, 26 and 19 days, 63, 12 to 20 and 22 to 35 days, respectively; and for the third generation, 38 and 27 days, 81, 171 to 281 (eggs overwinter), and 27 to 34 days, respectively (Charizanov, 1970).

As a method for trapping leafhoppers to check the percent infective individuals, Schwarz (1959) recommended placing yellow sheets under plants; these plants attracted four times more visiting *M. laevis* than control ones. Males were more attracted by yellow colour than females (at a rate 4:1).

Most importantly, *M. laevis* was shown to be a vector of yellows (mycoplasma) diseases, as first reported by Heinze and Kunze (1955) who transmitted the so-called European aster yellows (EAY) (Fig 6) with *M. laevis* in Germany. According to Valenta and Musil (1963), EAY was similar to clover dwarf (CD) or parastolbur. Musil and Valenta (1958) concluded that *M. laevis* was a vector of stolbur and apparently also of clover phyllody (CP) in Czechoslovakia. Then, Valenta (1961) reported that *M. laevis* transmitted stolbur, CP, and CD. In England, Harpaz (1964) used *M. laevis* to transmit CP and another disease agent of clover that did not induce greening of flowers and which was also transmitted by *Euscelis lineolata* Brullé. A yellows disease agent of onion was transmitted by *M. laevis* in Czechoslovakia (Novák, 1961) and in Poland where it was called EAY (Kochman and Książek, 1964). The Polish authors obtained transmission of EAY agent from onion or *Erigeron canadensis* L. to *Vinca rosea* L. using *M. laevis*. In Czechoslovakia, Mokra (1964) succeeded in transmitting the virescence agent of *Primula denticulata* Sm. to *Primula malacoides* Franch., which is a winter host of the disease, using

Fig. 6. The so-called European aster yellows in aster (right) and a healthy inflorescence of the same aster variety (left) (photograph by J. Brčák).

M. laevis. She also reported that leafhoppers collected outdoors on various plants infected with yellows diseases transmitted a yellows agent to *P. malacoides.*

The palearctic species *M. laevis* is similar to the North American species *Macrosteles fascifrons* (Stål), but an attempted crossing of the two species failed (Maramorosch, 1958d). Further experiments showed that *M. laevis* was unable to transmit either the Eastern or Californian strains of aster yellows. This implied that EAY had not been introduced into Europe from America. On the contrary, *M. fascifrons* transmitted both American strains of aster yellows and the EAY agent (Maramorosch, 1960).

Transmission of CD by *M. laevis* has been studied in some details. Musil (1966a) demonstrated a latent period for CD in the vector of 31 to 45 days. *M. laevis* (but not *Euscelis plebeja* (Fallén) easily infected *Stellaria media* (L.) Vill. with CD; the transmission efficiencies of the two species were apparently influenced by different trophic relations to the test plants. A reverse phenomenon was observed with *Trifolium repens* L., which could be easily infected with CD by *E. Plebeja*, but not by *M. laevis*. Musil (1975) demonstrated transmission of CD-agent by *M. laevis* but not the other yellows diseases tested, i.e. CP, parastolbur, dandelion virescence, and metastolbur. In his experiments, *M. laevis* transmitted CD to *Hordeum distichum* L., *Avena sativa* L., and *Poa annua* L. An aster-yellows-like agent transmissible by *M. laevis* was isolated from naturally infected *Poa annua* plants showing profuse tillering and dwarfing. The agent is transmissible to barley, *Hordeum distichon* L. (Murtomaa and Valenta, 1968); however, in Slovakia, this disease was not spread by *E. plebeja*, which, as shown by Musil (1975), was able to transmit CD to the gramineous species mentioned above.

In 1964, in northern Slovakia, Vacke (1966a) discovered two other diseases of oats in which 30 to 90% of plants in affected fields were diseased. These diseases differed from the oat sterile dwarf and wheat striate mosaic diseases and were not transmissible either by *Javesella pellucida* (Fabricius) or *Psammotettix alienus* (Dahlbom). The principal symptoms in oats were dwarfing and stripes. Both diseases were transmitted (with single or mixed infections) by *M. laevis*. The oat dwarf disease agent showed a latent period of three to four weeks in *M. laevis*, and 18 to 25% of leafhoppers were infective. It was transmitted to oats, barley, wheat, rye, bromegrass, and to *Stellaria media* (L.) Vill., spinach, and flax plants (Vacke, 1972). The symptoms in some plant species were reminiscent of the oat blue dwarf that occurs in N. America, but the oat dwarf agent induced distinct symptoms in wheat and rye plants. Vacke (1972) concluded that the oat dwarf disease might be related or identical with the oat blue dwarf disease described in America. Using electron microscopy, he has observed virus particles in infected oat plants (Vacke, personal communication). Therefore, he suggests that the disease agent of oat dwarf is the oat blue dwarf virus (OBDV). In central Slovakia and also in Moravia, OBDV causes flax crinkle disease and is transmitted by *M. laevis* (Vacke, 1970b). Flax crinkle is not related to flax virescence in *Linum austriacum* L. which is caused by a mycoplasma agent (Westphal and Heitz, 1971). The OBDV transmitted by *M. laevis* was found in 1970 in some localities of the Wroclaw province of Poland by Hoppe and Vacke (1972b).

The second disease, tentatively called oat stripe disease, is also transmitted by *M. laevis* (Vacke, 1966a) and is apparently caused by a mycoplasma agent. Vacke (personal communication) observed mycoplasmalike bodies in ultrathin sections of diseased plants and obtained remission of symptoms with tetracycline treatment. Therefore, the disease was named cereal yellows. Vacke (1970a) reported a latent period of this yellows agent in *M. laevis* of 2 to 5 (usually 3 to 4) weeks. Leafhoppers retained their infectivity until the death. Seventy percent of leafhoppers were able to transmit the cereal yellows agent to oats, barley, rye, wheat, *Poa annua* L., *Bromus arvensis* L., aster, spinach, carrot, *Vinca rosea* L., *Matricaria chamomilla* L., and *Plantago major* L.

In Czechoslovakia, Vacke (1973) reported transmission of the wheat pale green dwarf disease agent by *M. laevis* and *P. alienus* (cf. section 3.25 on *P. alienus*).

Blattný (1957, 1958, 1959) reported that the so-called pseudoclassic stolbur (including a yellows disease of *Anagallis arvensis* L.) was transmitted by *M. laevis* and *J. pellucida*. Both hopper species were implicated as vectors of witches' broom of pine as well by Blattný *et al.* (1970). To date, no one has confirmed these results.

Finally, a curious result was published by Kochman and Książek (1964) who reported that *M. laevis* presumably mechanically transmitted the onion yellow dwarf virus. However, this virus, having elongated particles, is normally stylet-borne by aphids. These results has not yet been confirmed.

3.17 *Macrosteles sexnotatus* (Fallén)

The European six-spotted leafhopper, *M. sexnotatus*, a ubiquitous species in Europe and Asia occurs frequently in many countries. Posnette and Ellenberger (1963) infected only one white clover plant with Delphinium yellows using *M. sexnotatus*. In the Netherlands van Slogteren and Muller (1969) proved *M. sexnotatus* transmitted an aster yellows-like agent. Van Slogeren and Muller (1972) succeeded in transmitting the agent causing "Lissers" hyacinths to *Vinca rosea* L. using *M. sexnotatus*. Infected plants developed the same symptoms as those inoculated with the agent from yellows infected gladiolus plants. Transmission of the pathogen from "Lissers" hyacinths to both healthy hyacinths and gladiolus plants was successful as well "Lissers" is apparently caused by a mycoplasma agent related or identical to that causing gladiolus yellows.

In Italy, Belli *et al.* (1972) tested *M. sexnotatus* as a possible vector of rice yellows (*giallume del riso*) which is presumably caused by a mycoplasma agent (cf. also Amici *et al.*, 1973).

3.18 *Euscelis plebeja* (Fallén)

The dwarf leafhopper, *E. plebeja*, is a palearctic species recorded in many European countries. It is one of the most common leafhopper species in France, Switzerland, Hungary, Czechoslovakia, etc. In Bulgaria, it was reported by Dirimanov and Charizanov (1965). Two or three generations a year were reported. Cousin (1968) in France, and Gáborjányi and Sáringer (1967) in Hungary reported two generations. In Hungary, Kuroli (1972b) observed maximum populations of adults by the middle of August. Dlabola (1954) found *E. plebeja* to be an abundant leafhopper species on meadows, fields, bushy vegetation, wet pastures, and especially on clover and alfalfa. *E. plebeja* occurs in the mountains as well. *E. plebeja* overwinters in late nymphal instars.

E. plebeja was one of the first and most studied leafhopper vectors in Europe. Musil (1965) described a method for rearing it. Lehmann and Claus (1970) elaborated on a method for characterizing the nutritional fitness of various plant species for *E. plebeja*. The method was based on the mortality rate of leafhoppers on different plants. Females survived longer than males. Following host plants were shown as suitable for *E. plebeja: Trifolium repens* L., *Chrysanthemum carinatum* Schousb., *Vicia faba* L., *Senecio vulgaris* L., and *Pisum sativum* L. Unsuitable hosts were *Rubus fruticosus* L., *Lycopersicon esculentum* Mill., *Mentha rotundifolia* Huds., *Fragaria ananassa* Duch., *Callistephus chinensis* Nees., and *Bromus inermis* Leysser. Some of these results contrasted with observations of natural yellows infections, e.g. of aster or strawberry plants. Also attempts were made to rear *E. plebeja* on artificial diets. In this way, Schäller (1972) succeeded in rearing *E. plebeja* from the first nymphal instar to adulthood in 60 to 70 days (which normally takes 30 days); he hypothesized that the main problem of artificial rearing was the absence of symbionts in the artificial diet.

In the Netherlands, Maramorosch (1953) provided evidence that *E. plebeja*, obtained by sweeping crimson clover, harbored an agent causing a previously unknown clover disease. (Some other authors have called it European clover stunt or clover enation mosaic. The same or very similar symptoms were described in Czechoslovakia by Musil and Kvíčala (1973) with the clover rough vein disease, the agent of which was isolated by the aphid *Acyrthosiphon pisum* Harris from naturally infected red clover plants. Four aphid species but not *E. plebeja* transmitted this non-sap-transmissible agent, which was thought to be a mycoplasmalike organism; however, the available electron micrographs are inadequate for confirming this. Furthermore, Evenhuis (1958a) proved a toxic effect in clover plants caused by substances excreted in saliva by *E. plebeja* which simulated some symptoms of the first described disease; however, no such effect of *E. plebeja* saliva was found by Musil and Kvíčala (1973).

E. plebeja was found to transmit two diseases of clover (mild crinkle and chlorotic stunting) by de fluiter *et al.* (1955). Then, in the Netherlands, Evenhuis (1958a) reported an agent from clover, unlike aster yellows, transmitted by *E. plebeja*, and probably the same as that which causes green petal of strawberry.

Until now, all plant diseases found to be naturally transmitted by *E. plebeja* were of mycoplasma origin. There may be some doubt, however, with the yellows disease of grapevine transmitted to *Vicia faba* L. by *E. plebeja.* Whether this agent is a rickettsialike organism or a virus remains obscure (Küppers *et al.*, 1975). Also, the eitology of the histoid enation disease of cereals, resembling the oat sterile dwarf virus or maize rough dwarf virus diseases, and transmitted by *E. plebeja* in west Turkey, has not been clarified (Bremer and Raatikainen, 1975). These authors found that in west Turkey the barley yellow stripe disease agent was transmitted by *E. plebeja* as well and it differed somewhat from the European wheat striate mosaic. The barley yellow stripe agent had a latent period of 20 to 26 days in *E. plebeja.*

E. plebeja may be a carrier of agents which it does not transmit naturally. For example, it is able to acquire the beet leaf curl virus (*Kräuselkrankheit der Rube*) which persists in its body for some time (Proeseler, 1966). This virus is naturally transmitted by the bug *Piesma quadratum* (Fieb.). Daniel *et al.* (1973) obtained transmission of a spiroplasma associated with the citrus little-leaf disease to clover by means of *E. plebeja* injected with cultured spiroplasma. Markham *et al.* (1974) succeeded in isolating this agent from leafhoppers. However, *E. plebeja* was unable to acquire the spiroplasma by feeding on infected plants or to act as a natural vector. Even *Acholeplasma laidlawii* survived for at least ten weeks after being injected into *E. plebeja* leafhoppers.

In England, *Trifolium repens* L. plants showing symptoms similar to clover club leaf were found and rickettsialike organisms were observed in their phloem cells. An attempted transmission of the pathogen by *E. plebeja* failed (Markham *et al.*, 1975).

Plant pathogenic mycoplasmas (many which were formerly considered to be viruses of the yellows-type group) cause diseases in many wild and cultural plants.

Usually it is not easy to prove their identity or differences among them on the basis of older or obsolete data. *E. plebeja* is able to transmit only some of them. For example, it was unable to transmit the pathogen causing tillering and dwarfing of *Poa annua* L. in Czechoslovakia which is transmitted by *Macrosteles laevis* (Ribaut) (Murtomaa and Valenta, 1968). Symptoms of this disease resembles those of clover dwarf, which has been shown to be transmitted by *E. plebeja* (Musil, 1975). *E. plebeja* transmits some yellows diseases infecting barley, wheat, and oats in west Turkey (Bremer and Raatikinen, 1975). In such cases, a precise strain or species determination of pathogens is practically impossible. Only some mycoplasma agents have characteristics definitive enough to allow their being related to the particular diseases they cause in different plants. Hitherto, these pathogens have been categorized on the basis of their biological properties.

3.18.1 Clover Phyllody

E. plebeja was shown to be vector of clover phyllody (CP) in England by Frazier and Posnette (1957). CP is also transmitted by other leafhoppers. In Switzerland, Bowey (1957) found that both *E. plebeja* and *Aphrodes bicincta* (Schrank) transmitted CP. Valenta (1961) in Czechoslovakia, and Posnette and Ellenberger (1963) in England, showed that CP was transmitted by *E. plebeja, A. bicincta,* and *Macrosteles laevis* (Ribaut). Giannotti (1969b) reported in France that *E. plebeja* as well as *Euscelidius variegatus* (Kirschbaum) transmitted CP. In Italy, Belli *et al.* (1972) confirmed Grancini's (1962) results on transmission of CP by *E. plebeja* and reported that *A. bicincta* was another vector.

In Belgium, Vanderveken (1965) and, in France, Cousin and Moreau (1966) proved that the CP agent passes the winter not only in clover plants but also in overwintering nymphs of *E. plebeja.* Ploaie (1966) reported the CP vector *E. plebeja* from hilly and undermountains areas of Roumania, thus concurring with Savulescu and Ploaie (1964, 1967) who mentioned a strong incidence of CP, *E. plebeja*, and *A. bicincta* in the Transylvania Plateau (at 300 to 800 m above sea level) with a wet climate, in contrast to the Roumania Plain, where only single individuals of both leafhoppers could be found.

In the German Democratic Republic, Lehmann (1971, 1973a) isolated CP from white clover by means of *E. plebeja*. He obtained CP symptoms in plants infested with *E. plebeja* leafhoppers which had acquired the agent from other plants. In Kuroli's (1972b) experiments in Hungary, *E. plebeja* transmitted CP to *Trifolium repens* L. and to *Trifolium pratense* L. CP also occurs in Yugoslavia. The strawberry green petal disease (caused by the CP agent) was reported by Perišić (1960), and CP infection in clover plants was reported by Grbelja and Ljubešić (1975). CP was found in Denmark and Lithuanaian S.S.R. as well. In trials using *E. plebeja* Musil (1964a) succeeded in infecting twenty plant species with CP.

Musil (1961, 1964a) stated that the latent period of CP agent in *E. plebeja* was approximately one month and that minimum threshold period was 22 to 24 days. In contrast, Vago and Giannotti (1972) reported a minimum threshold period of only 12 to 15 days. The duration of the latent period is temperature

dependent. The latent period is a week longer when the temperature is lowered from 24 to 20°C, and another one or two weeks longer when it drops to 15°C. At 10°C, the CP agent remains latent in the leafhopper. Musil (1961) determined that 30 to 60% of leafhoppers were inoculative in his experiments. The natural infectivity of *E. plebeja* is usually very high with yellows diseases in white clover. In France, Gondran (1967) reported 37 to 36% infective leafhoppers. Under experimental conditions 92 to 100% of *E. plebeja* individuals acquire and transmit the CP agent (Musil, 1964b). The transmission of CP depends considerably on the species of hosts plants and on temperature. In Musil's (1965) experiments, a 3-day acquisition period at 24°C resulted in 90% infective leafhoppers, while at 10°C only 44% of *E. plebeja* transmitted CP. With CP transmission by *E. plebeja* irregularities were observed as expressed by discontinuous inoculativity, sometimes by loss of inoculativity at the end of life, and by individual variations (Cousin, 1968; Cousin *et al.*, 1968; Lehmann *et al.*, 1970).

Musil (1963) observed that after a prolonged maintenance CP agent in plants (without transmission by leafhoppers), CP transmissibility by *E. plebeja* dropped little by little. After maintaining CP in *Trifolium repens* L. for 3 yr, all 165 individual *E. plebeja* kept for 40 days on those plants failed to transmit CP.

The CP agent (or stolbur agent as well) does not lose infectivity at a low temperature. Musil (1964c) kept frozen infective leafhoppers at -20°C for 22 days. Inocula prepared from those frozen insects and injected into healthy *E. plebeja* rendered them infective. Thus, this method offered a possibility of maintaining stored yellows agents. Otherwise, the CP agent remained infective in extracts from crushed infective leafhoppers for maximum of 7 hr (Musil, 1964e).

Musil (1964d) achieved four serial transfers of CP (stolbur and parastolbur as well) agent by injecting successively healthy *E. plebeja* individuals with hemolymph taken originally from infective leafhoppers. In this way he obtained evidence of multiplication of CP agent in the vector. Giannotti *et al.* (1969b) infected leafhoppers (*E. plebeja* and *E. variegatus*) with CP mycoplasma extracted from phloem fragments of diseased *Vinca rosea* L. plants. In the same way he obtained transmission of the stolbur C mycoplasma to *E. plebeja*. The two leafhopper species were also used for experiments by Faivre-Amiot *et al.* (1970) who succeeded in infecting nymphs of the last two instars and adults of *E. plebeja* by injections or by feeding leafhoppers through a parafilm membrane with CP agent cultivated in an acellular, semisynthetic medium. Also, Kleinhempel *et al.* (1974) injected a white clover *Acholeplasma* isolate from bouillon cultures into *E. plebeja* and obtained back isolation of this agent from leafhoppers after 48 days. Lehmann (1973a) injected the juice from green petal flowers of *Hydrangea macrophylla* DC. into healthy *E. plebeja* leafhoppers, which then transmitted CP agent to *Chrysanthemum carinatum* Schousb.

Lehmann (1971) succeeded in reducing and temporarily halting the vector ability of *E. plebeja* by injecting the leafhoppers with a 0.1% solution of tetracycline-hydrochloride.

Giannotti *et al.* (1968d) reported degeneration of mycoplasma bodies both in CP infected vectors and plants. They concluded that this might be a sign of recovery (within plants) and of immunological reaction (within leafhoppers), and might also explain the loss of transmitting ability in aged vectors. MLO's may be pathogenic to vectors. Giannotti *et al.* (1968a) and Giannotti and Devauchelle (1969), using cytochemical staining techniques, observed in CP-invaded *E. plebeja* cytoplasmic lesions in various tissues which were interpreted as cell injuries caused by mycoplasma.

Individual *E. plebeja* injected with CP agent, taken from primocultures in which it multiplied, showed latent periods of 10 to 28 days after which 35 to 86% of the leafhoppers transmitted CP to plants (Giannnotti *et al.*, 1971). Similar results were reported by Giannotti (1972) with two strains of CP.

Giannotti *et al.* (1973) observed mycoplasma bodies accompanied by rods 160 to 170 nm long and 31 nm in diameter in midgut cells of CP-infected *E. plebeja*. The rods were thought to represent either a particular state of mycoplasma or a new type of virus or a mycoplasma phage. Similarly, mycoplasma bodies were also accompanied by rodlike particles in plants infected with other mycoplasmas. In stolbur SM infected plants, the rods were numerous in degenerating mycoplasma bodies and extruded from mycoplasma bodies through the unit membrane.

Giannotti *et al.* (1970) and Ionica (1970, 1971) attempted to infect "in vitro" isolated organs of healthy *E. plebeja* with CP agent. Healthy salivary glands "*in vitro*" were infected with inocula taken from salivary glands or abdomens of infective leafhoppers. Evidence of the infection was provided by injecting healthy leafhoppers with crushed glands previously infected and incubated "in vitro." Those leafhoppers transmitted CP to plants.

3.18.2 Clover Dwarf

The mycoplasma etiology of clover dwarf (CD) disease was proved by Ploaie and Maramorosch (1969). CD has been investigated in Czechoslovakia, Italy, and the German Democratic Republic. It has also been found in Hungary [Horváth (1969) mentioned CD in rape (*Brassica napus* L.)]. Identity of other described yellows diseases with CD is difficult to prove.

Under natural conditions, *E. plebeja* was shown to be an efficient vector of CD (Musil, 1960). The CD agent multiplies in its vector *E. plebeja* as demonstrated by Musil (1962a, 1964bd) using the serial-transfer method. Small volumes (approximately 5×10^{-5} to 1×10^{-4} ml) of undiluted hemolymph was withdrawn from inoculative leafhoppers and sequentially injected into healthy ones. The CD agent was transferred in this way through 4, 7, or 10 passages. Then, individuals of *E. plebeja* that were inoculated with inoculum in the 10th passage were tested on white clover plants for inoculativity. The relative concentration of CD agent in the hemolymph of infective leafhoppers in the 10th passage was ascertained by comparison with the dilution end-point of the agent in hemolymph. The concentrations of CD agent in injected insects showed no decrease in the course of serial passage, thus confirming multiplication in the vector. The latent period of CD agent in

leafhoppers injected with hemolymph diluted 1:100 was longer than in those injected with 1:10 dilutions. At 22°C, extracts from dissected or macerated vectors diluted 1:10 or 1:100 lost their infectivity after 2 hr (Musil, 1964e).

The average latent period of CD agent in *E. plebeja* observed by Lehmann (1969b) was 28 days, Musil (1964a) reported a minimum latent period of CD in *E. plebeja* of 26 days and a maximum of 47 days. Discontinuous inoculativity and loss of inoculativity towards the end of life were observed with some individuals. The latent period of CD agent in *E. plebeja* was shorter with younger nymphs than with older nymphs or adults and it was longer at 20°C than at 27°C (Musil, 1965).

Temperature also influenced the infectivity of CD in *E. plebeja*. Musil (1965) found that 87% of *Senecio vulgaris* L. were infected at 25°C and only 61% at 15°C. However, the results were different when *Trifolium pratense* L. and *Chrysanthemum carinatum* Schousb. were used. After a three-day acquisition-access feeding, 20% or 40% of leafhoppers transmitted CD at 10 or 24°C, respectively. Presumably a minimum of 2 to 5 min was sufficient for inoculation, but leafhoppers kept on test plants for a longer period were more efficient. Maximum transmission was obtained after 6 to 7 days. This phenomenon may be explained hypothetically by discontinuous inoculativity, by a nontransmissible state of mycoplasma within the vector body, by insufficient doses of the agent, or by poor infection sites on plants exposed to inoculation by leafhoppers.

CD agent can be acquired by *E. plebeja* from plants before they show symptoms of CD (like clover phyllody, CP). Factors affecting acquisition of CD agent by leafhoppers were investigated by Musil (1963, 1965): Acquisition periods of 1, 3, and 6 days on a CD source plant resulted in 6, 12, and 33% of infective *E. plebeja* respectively. (However, such differences were not observed with the CP agent). The length of the acquisition period together with the phase of infection in CD-infection sources influenced the infectivity of *E. plebeja* as follows: Leafhoppers given 2-day acquisition feeds on *Trifolium repens* L. infected 14 or 45 days previously resulted in 43 and 4% individuals transmitting the CD agent, respectively. Six-days of acquisition feeding on the same plants resulted in 55 and 12% infective leafhoppers, respectively. The highest rate of CD acquisition (60%) occurred with nymphs of the first to third instars, 40 to 50% with the fourth and fifth instars, and 29% with adults. No significant differences occurred between males and females.

Clover dwarf can be transmitted by *Macrosteles laevis* (Ribaut) and *Aphrodes bicincta* as well (Valenta, 1961). In nature, CD evidently infects many plant species, e.g. some ornamental plants, rape (*Brassica napus* L.) and others. Lehmann (1969ab, 1971) obtained transmission of transmitted agents closely related to CD to *Trifolium repens* L. using *E. plebeja*. Lehmann and Skadow (1971) transmitted only the CD agent from naturally infected winter rape plants. However, winter rape can also be artificially infected with clover phyllody which induces same symptoms (green petal or phyllody) as CD. Musil (1964a) transmitted CD to 22 plant species. He (Musil, 1975) also found that *E. plebeja* (and also *M. laevis*) could transmit CD (but not CP, parastolbur and dandelion virescence) to gramineous plants

(*Hordeum distichum* L., *Avena sativa* L., and *Poa annua* L.). This result may be very important in the epidemiology and identification of yellows diseases in cereals.

3.18.3 Stolbur

Musil (1959) obtained transmission the stolbur agent to ten plant species using *E. plebeja* as a vector. *Trifolium repens* L. was very susceptible, whereas *Stellaria media* (L.) Vill. could hardly be infected. Individuals of *E. plebeja* infected 72% of *T. repens* plants on the average. Other yellows agents were more efficiently transmitted by *E. plebeja* than stolbur and to more plant species (Musil, 1964a). Kuroli (1972b) was unsuccessful in transmitting stolbur agent with *E. plebeja* in Hungary. According to Posnette and Ellenberger (1963), stolbur was occasionally transmitted by *E. plebeja* in England.

Giannotti (1972) injected mycoplasma agents of stoblur C and SM cultivated "in vitro" into *E. plebeja* leafhoppers which were tested afterwards for infectivity on clover plants. In this way, the test plants were infected with the stolbur C but not with the stolbur SM.

3.18.4 Parastolbur

Valenta (1961) reported that *E. plebeja* was a vector of parastolbur and Valenta and Musil (1963) reported an additional vector, *Aphrodes bicincta* (Schrank). The mycoplasma etiology of parastolbur was demonstrated by Ploaie and Maramorosch (1969).

The transmission efficiency of *E. plebeja* varied with different plant species; 23 species showed susceptibility to parastolbur agent, but some of them e.g. aster, tomato and potato plants were only rarely infected. These differences might be caused by trophic relations of the vector because, otherwise, 70% of these leafhoppers were infective on the average (Musil, 1962b, 1964a, 1975). As reported in these papers, the latent period of the parastolbur agent (22 to 33 days) was longer than those of clover phyllody and clover dwarf. The shortest latent period was observed at 25°C, and lower temperatures prolonged it. A 3-day acquisition at 24°C or at 10°C resulted in 90 to 50% of infective leafhoppers, respectively. *E. plebeja* leafhoppers allowed to feed one or three days on parastolbur infected plants, resulted in 43 or 93% of inoculative individuals, respectively. Musil (1966b) demonstrated mechanical transmissibility of parastolbur agent from leafhoppers to leafhoppers by means of the injection method. Infectivity of extracts obtained from infective *E. plebeja* was diminished by heating. An extract heated at 35°C for 30 minutes rendered 13% of injected leafhoppers infective. Extracts kept at 40°C for 10, 20, and 30 min reduced infectivity of leafhoppers to 43, 12, and 18% respectively; and the latent period was prolonged for an additional 10 or more days (until 45 days). The infectivity of extracts was lost at 45 or 50°C.

3.18.5 Other Yellows Diseases, Their Complexes, and Notes

Transmission of yellows disease agents by *E. plebeja* does not depend merely on their coherency to *E. plebeja* but also on trophic relations of the vector to var-

ious plant species. For instance, *E. plebeja* can easily infect *Vinca rosea* L. with clover phyllody (CP) or clover dwarf (CD), but it hardly acquires these agents from *V. rosea* (Musil, 1965). Usually individual yellows diseases were differentiated according to their host range, symptoms, specificity of vectors, interference phenomena, and distribution. There is also a great deal of difference in vector efficiency with different agents. In Musil's (1964a) experiments *E. plebeja* transmitted yellows agents with following efficiencies: CP - 92 to 100%, parastolbur - 70%, CD - 58%, and stolbur - 9%.

Moreover, *E. plebeja* is able to transmit the agents of dandelion virescence (a yellows disease of *Taraxacum officinale* Web.) and metastolbur (Musil, 1969, 1975). Valenta and Musil (1963) described a yellows disease of *Senecio vulgaris* L. that was transmitted by *E. plebeja* as well. The highest susceptibility to the yellows disease was found with *Senecio vulgaris* L. (81.6%), lower ones with *Sonchus oleraceus* L. (62.5%), *Taraxacum officinale* Web. (39%), *Trifolium pratense* L. (32.7%), *Anagallis arvensis* L. (9.5%), and aster (2.5%). Presumably, the length of feeding affected the transmission rate, because infective *E. plebeja* leafhoppers allowed to feed for 7 days on test plants (*Trifolium repens* L.) infected 92.2% of plants, while those fed for 1 or 2 days on test plants infected only 56.5% of them.

E. plebeja was also employed for separating yellows agents from complex infections. For example, CP symptoms in *Trifolium repens* L. are masked by parastolbur infection, and *E. plebeja* transmits both agents from doubly infected plants. However, the CP agent has a shorter latent period in *E. plebeja* than the parastolbur agent, and, consequently, may be separated on the basis of this differential latency. It is also possible for *E. plebeja* to acquire successively both agents (Musil, 1965). This paper reported, moreover, that the loss of inoculativity induced by high temperatures with *E. plebeja* might be temporary, because when the temperature was lowered the agents (CP, CD, parastolbur) apparently multiplied to an infectious titer in leafhoppers.

Mycoplasma bodies occur in salivary glands apparently just at the end of the latent period. This period may be shorter with leafhoppers which acquired the agent by injection rather than by feeding on infected plants. Stanarius *et al.* (1976) proved that mycoplasma bodies could be found in the salivary glands of *E. plebeja* first 25 days after injection with crude sap from proliferation affected *Vinca rosea* L. plants; a large amount of mycoplasma bodies were found in salivary glands after 45 days.

Evidently, *E. plebeja* is not a universal vector of all mycoplasma agents infecting plants. Giannotti (1972) found that: not every mycoplasma isolate cultivated "*in vitro*" and then injected into *E. plebeja* individuals rendered them inoculative.

Posnette and Ellenberger (1963) reported occastional transovarial transmission of clover witches' broom and strawberry green petal agents in *E. plebeja*. No one, to date, has confirmed these results.

In experiments by Posnette and Ellenberger (1963) *E. plebeja* transmitted strawberry green petal from infected strawberry plants to other hosts but not to strawberry plants. Other results suggested that the clover witches' broom agent

interfered with the ability of the leafhopper *E. plebeja* to acquire or transmit the strawberry green petal agent. The clover witches' broom agent retared the development and hatching of *E. plebeja's* eggs and apparently reduced the longevity of adults.

3.19 *Euscelis lineolata* Brullé

This species has been found principally in Western Europe, Pelov (1968) also reported it from Bulgaria. Frazier and Posnette (1956, 1957) ascertained that *E. lineolata* transmitted two mycoplasma diseases in England, the clover phyllody (CP) (or strawberry green petal) and clover witches' broom. Both seasonal variants of *E. lineolata*, named *Euscelis bilobatus* Wagner and *Euscelis galiberti* Ribaut, acted as vectors as well. In the Netherlands, Evenhuis (1958a) using *E. lineolata* transmitted what was probably CP agent. In England, the CP agent was detected by Harpaz (1964) in *E. lineolata* leafhoppers collected in the field.

Maillet (1970a) investigated the infection process of CP mycoplasma in *E. lineolata* and reported the passage of mycoplasma by endocytosis from extracellular phase (within hemolymph) to the intracellular phase (into cells of salivary glands). In cells, peripheral invaginations originated containing mycoplasma bodies; plasmalemma of a secretory cell was pushed into the cell and formed many protrusions between the mycoplasma bodies. Finally, vacuolar formations originated by endocytosis. Gouranton and Maillet (1970, 1973) using autoradiography and electron microscopy proved that the CP agent multiplied in cytoplasm of foregut cells of *E. lineolata*. Another high resolution autoradiographic study showed that after tritiated thymidine injection the mycoplasma bodies were labeled in the digestive tract epithelium, the hemolymph, and the salivary gland; their multiplication was shown to occur both with intracellular and extracellular bodies. Maillet and Gouranton (1970, 1971, 1974) also demonstrated multiplication of CP mycoplasma in hypertrophic cells of the filter chamber; some of which showed necrosis in advanced stages of infection; other cells were not necrotic, although they contained many mycoplasma bodies. Envacuolized mycoplasma bodies probably pass from those cells into the leafhopper hemolymph. Thirty seven days after acquisition by feeding, mycoplasma bodies appear in salivary glands and in saliva as well. These cytological and autoradiographic studies showed that mycoplasma multiplied, particularly in midgut and salivary glands cells.

Besides mycoplasma bodies rickettsialike organisms (RLO) were discovered by Maillet (1970b, 1970c) in salivary glands and saliva of the CP vector *E. lineolata.* However, authors are usually puzzled by these RLO's which may represent either pathogens or symbionts of leafhoppers. Maillet also evokes some older references (since 1923) on RLO's in insects in context with epizootics and further findings of RLO's in nonvector Homoptera.

Finally, Gourret *et al.* (1973) discussed an association of rod-shaped, viruslike particles, smaller than those reported by Giannotti *et al.* (1973), with CP agent in *Euscelis plebeja* (Fallén). Mycoplasma bodies occurred together with the viruslike particles in salivary gland cells or free in the hemolymph of the CP vector *E. lineo-*

lata and in phloem cells in root nodules of CP-infected *Trifolium repens* L. If the rod-shaped particles were viruses, they would presumably infect the mycoplasma and not the plant, because they occurred both in infected insects and infected plants.

3.20 *Euscelidius variegatus* (Kirschbaum)

This palearctic species was introduced from Europe into North America. Severin (1947) demonstrated that it could transmit the aster yellows agent. In some European countries, this leafhopper species occurs only rarely, e.g. in Czechoslovakia it is reported only from some warm localities. Dlabola (1954) suggests that its occurrence in Czechoslovakia is doubtful.

In France, *E. variegatus* was ascertained as a new clover phyllody (CP) vector by Giannotti *et al.* (1969a). Sixty-two percent of *E. variegatus* individuals transmitted CP between the 16th to 40th day after acquisition. *E. variegatus* and *Euscelis plebeja* (Fallén) showed similar transmission efficiencies in the same conditions. Some laboratory and field observations suggested a somewhat different host range of *E. variegatus* as compared with *E. plebeja* and *Aphrodes bicincta* (Schrank). In *E. variegatus* reared on CP infected clover Giannotti (1969a, 1969b) (cf. also Vago and Giannotti, 1972) found, in addition to CP mycoplasma bodies, the same cellular modifications described with *E. plebeja* and *A. bicincta* (cellular lesions were observed in midgut, salivary gland, aorta and epithelial cells. As already mentioned in section 18 on *E. plebeja*, Giannotti *et al.* (1969b) and Faivre-Amiot *et al.* (1970) successfully used *E. variegatus* for artificial acquisition of CP agent.

3.21 *Idiodonus cruentatus* (Panzer)

The European species *I. cruentatus* occurs frequently in Czechoslovakia, especially in hilly and undermountain areas, on forest clearings and sunny hillsides, in shrubs and associated vegetation in July and August (Dlabola, 1954). In Bulgaria, it was collected on roses and blueberry plants (Pelov, 1968; Charizanov, 1969).

In Czechoslovakia, Blattný (1963/64) reported that, in his experiments, *I. cruentatus* transmitted the witches' broom disease of blueberry (*Vaccinium myrtillus* L.) to two plants. There are no details on experimental circumstances in the paper and no confirmation of the results has been published.

The mycoplasma origin of *Vaccinium myrtillus* witches' broom disease was confirmed by means of electron microsocpy by Kegler *et al.* (1973) in Germany and by Leeuw (1975) in the Netherlands.

3.22 *Loepotettix dilutior* (Kirschbaum)

There is only one report by Posnette and Ellenberger (1963) on this leafhopper vector from England. A colony of *L. dilutior* collected from brambles was carrying a yellows agent causing stolbur symptoms in clover. No confirmation of this work has been reported.

3.23 *Scaphoideus littoralis* Ball

S. littoralis was introduced into Europe from North America. In Europe, it occurs at present in France, northern Italy and Switzerland (Baggiolini *et al.*, 1968). Nielson (1968) briefly describes the bionomics of this species which has one generation a year and is restricted to grapevines. Eggs of *S. littoralis* go through the diapause. More than three hundred herbaceous plant species were investigated as possible host plants for *S. littoralis*; some of them were more suitable for longer survival of *S. littoralis*, e.g. *Chrysanthemum coronarium* L. or *Cineraria maritima* var. *candidans*, etc. (Caudwell *et al.*, 1970). *S. littoralis* apparently feeds in phloem as well as in xylem (Carle and Moutous, 1965).

In Europe, *S. littoralis* transmits the agent of flavescence dorée of grapevines (FDG) as proved by Schvester *et al.* (1961). Also, in Italy, Vidano (1964) obtained flavescence dorée-like symptoms in grapevines after feeding of this leafhopper. The vector ability of *S. littoralis* has not been investigated in its native continent.

FDG was epidemic in southwest France in 1950. FDG occurs also in northern Italy (Belli *et al.*, 1972) and presumably in West Germany. Schvester *et al.* (1967) failed to find any fully resistant vine variety, although 23 varieties tested showed different degrees of susceptibility to FDG. Caudwell *et al.* (1970) stated that nymphs of *S. littoralis* could acquire the FDG agent, but adults were better at transmitting it. These authors succeeded in transmitting the FDG agent to *Vicia faba* L. and *Chrysanthemum carinatum* Schousb. The back transmission from *Vicia faba* was successful.

The mycopalsma agent of FDG was observed with the electron microscope by Caudwell *et al.* (1971) in infected tissues of vine, bean, and chrysanthemum, as well as in salivary glands of *S. littoralis* experimentally infected under controlled conditions.

In Germany, Küppers, *et al.* (1975) reported the yellows disease of grapevines (*Goldgelbe Vergilbung*) resembling FDG or "bois noir." The vector of the latter has not been found as yet. The yellows disease of grapevines was transmissible to *Vicia faba* L. by *Euscelis* leafhoppers and back to grapevine by *S. littoralis*. Symptoms of this yellows disease differred from that of FDG. Küppers *et al.* (1975) described both rickettsialike organisms (RLO) and viruslike particles with this disease, but they did not prove that either or both suspected agents were the cause of the yellows disease of grapevines.

RLO's were found also in grapevines showing symptoms of infectious necrosis by Ulrychová *et al.* (1975) in Czechoslovakia. Remission of symptoms of the infectious necrosis was achieved by penicillin treatment. No vector of this disease has been discovered. In my opinion, a relation of infectious necrosis to FDG can hardly be suggested; the disease resembles Pierce's disease from America more than anything else.

3.24 *Speudotettix subfusculus* (Fallén)

This species is able to transmit clover phyllody mycoplasma that causes strawberry green petal disease (Posnette and Ellenberger, 1963).

3.25 *Psammotettix alienus* (Dahlbom)

P. alienus is a common leafhopper species distributed in Europe and North America. In Bulgaria, it was reported by Dirimanov and Charizanov (1971). In Czechoslovakia, *P. alienus* represents one of the most prevalent leafhopper species in grasslands and fields. According to Nowacka (1975), *P. alienus* in Poland has two generations a year and is particularly abundant in cereals and seed cultures of cultivated grasses. *Psammotettix* species represent 40 to 65% of the entire hopper fauna in cultivated forage grasses (5 to 30% in cereals).

3.25.1 Wheat Dwarf Disease

In Czechoslovakia, Vacke (1961) and simultaneously Hesková *et al.* (1961) proved that *P. alienus* transmitted a disease agent causing an apparently undescribed disease named the wheat dwarf disease (WDD). The disease was thought to be caused by a virus presumably related to the Russian winter wheat mosaic virus. Both nymphs and adults of *P. alienus* transmitted WDD agent to spring wheat and spring barley with an efficiency of 73 to 82%. Vacke (1964a) showed that nymphs were more efficient vectors (up to 97%) than adults. The transmission efficiency of adults dropped with age of the individuals: at the age of 1 to 4, 10 to 13, and 23 to 26 days, 84, 66, and 58% of adults became infective, respectively. One single leafhopper was able to transmit WDD for 80 days, however, some individuals quickly lost infectivity and others were only intermittent inoculative. Five minutes of feeding was adequate for acquisition of the WDD agent; the latent period in nymphs of the 3rd and 4th instars was only 1 to 4 days. No transovarial transmission was found. Attempts to transmit the WDD agent by *Javesella pellucida* (Fabricius), *Laodelphax striatellus* (Fallén), and *Dicranotropis hamata* Boheman failed. On the other hand, *P. alienus* was unable to transmit the oat sterile dwarf virus (Vacke, 1964b). WDD may also occur in the Ukraine.

A disease assumed to be new, but closely resembling WDD and also transmissible by *P. alienus* was discovered by Radulescu and Munteanu (1970) in the Transylvania region of Roumaina. They named this disease the yellow stunting of wheat.

3.25.2 Band Mosaic of Wheat and Rye

In 1968, *P. alienus* was shown to be the vector of an infectious agent causing band mosaic of wheat and rye (BMWR) in Poland (Hoppe, 1969; Nowacka and Hoppe, 1969). The BMWR agent was not transmitted by *Javesella pellucida* (Fabricius) and *Macrosteles laevis* (Ribaut). The latent period of the BMWR agent in *P. alienus* varied between 19 and 25 days (15 to 23 days in plants). A BMWR closely related to or identical to a disease of winter wheat was recorded in Czechoslovakia by Vacke and Hoppe (1975) who also identified its only vector, *P. alienus*. The latent period of the agent in *P. alienus* leafhoppers was 14 to 35 days (usually 21 to 28 days) and the inoculativity of leafhoppers extended was life-long. Both nymphs and adults of *P. alienus* were able to transmit the agent. Symptoms in cereals (winter and spring wheat, spring rye, winter and spring barley, and oats) appeared within 15 to 25 days.

Hoppe (1974) and Nowacka (1975) mentioned that BMWR from Poland appeared to be the same as winter wheat mosaic. Hoppe (1974) characterized the relationship of the disease agent to *P. alienus* as follows: both nymphs and adults can act as vectors. In adults, the minimum acquisition feeding period is 15 min, but the highest transmission efficiency is obtained after a one day acquisition access period. The latent period in adults is three weeks on the average, the shortest may be 13 to 15 days, the longest 35 to 37 days. The minimum and maximum incubation periods in plants are 7 to 9 days and 27 to 29 days, respectively, and 14 days on the average. Higher temperatures and longer daylight reduced the latent period in leafhoppers. With some vectors a periodical loss of inoculativity was observed, but others remained inoculative until they died.

The highest incidence of the disease was observed in Poland in sparsely sown fields. Under field conditions, up to 76.4% of winter wheat was infected. In other cereals, except oats, the highest incidence was 30%. Fourteen gramineous species were found as susceptible in experiments by Hoppe (1974).

Hoppe (1974) concluded that the disease was identical to or a strain of the Russian winter wheat mosaic (RWWM). Nevertheless, the RWWM virus is transmitted by *Psammotettix striatus* (Linné) in the U. S. S. R. (cf. references in Nielson, 1968). It is difficult to distinguish *P. striatus* from *P. alienus* or to draw reliable conclusions concerning differences between the two diseases based solely on diverse vector species. *P. striatus* occurs sporadically in Poland (Nowacka and Hoppe, 1969); it was noted from Bulgaria (Pelov, 1968) and infrequently in Czechoslovakia, where when it occurs it is found especially at sandy locations (Dlabola, 1954). Of course, there are additional ways of comparing the two wheat diseases. For example, RWWM is transmitted transovarially and exhibits pathological effects in its vector. RWWM virus particles are bacilliform as shown by Razvjazkina *et al.* (1968), and Razvjazkina and Polijakova (1969).

3.25.3 Wheat Pale Green Dwarf Disease

The wheat pale green dwarf (WPGD) disease was described in Czechoslovakia by Vacke (1973). It infects rye, barley, and oats, resulting in dwarfing, abnormal tillering, pale green colour of leaves, and proliferation of floral bracts. *P. alienus* is a very efficient vector of WPGD and retains life-long inoculativity. The latent period of the WPGD agent in the vector is 21 to 28 days. Transmission through eggs of *P. alienus* was not proved. *Macrosteles laevis* (Ribaut) is also a vector of WPGD. Vacke (1973) presumes that the agent of WPGD is identical with a virus of winter wheat characterized by Agarkov (1966) in the U. S. S. R.

3.25.4 A Mycoplasma Agent

In Roumania, Ploaie *et al.* (1975) reported that *P. alienus* was a vector of a mycoplasma agent causing chlorosis, dwarf, and total or partial aspermy in wheat, barley, and oats and could also be transmitted to *Chrysanthemum carinatum* Schousb. and *Vinca rosea* L.

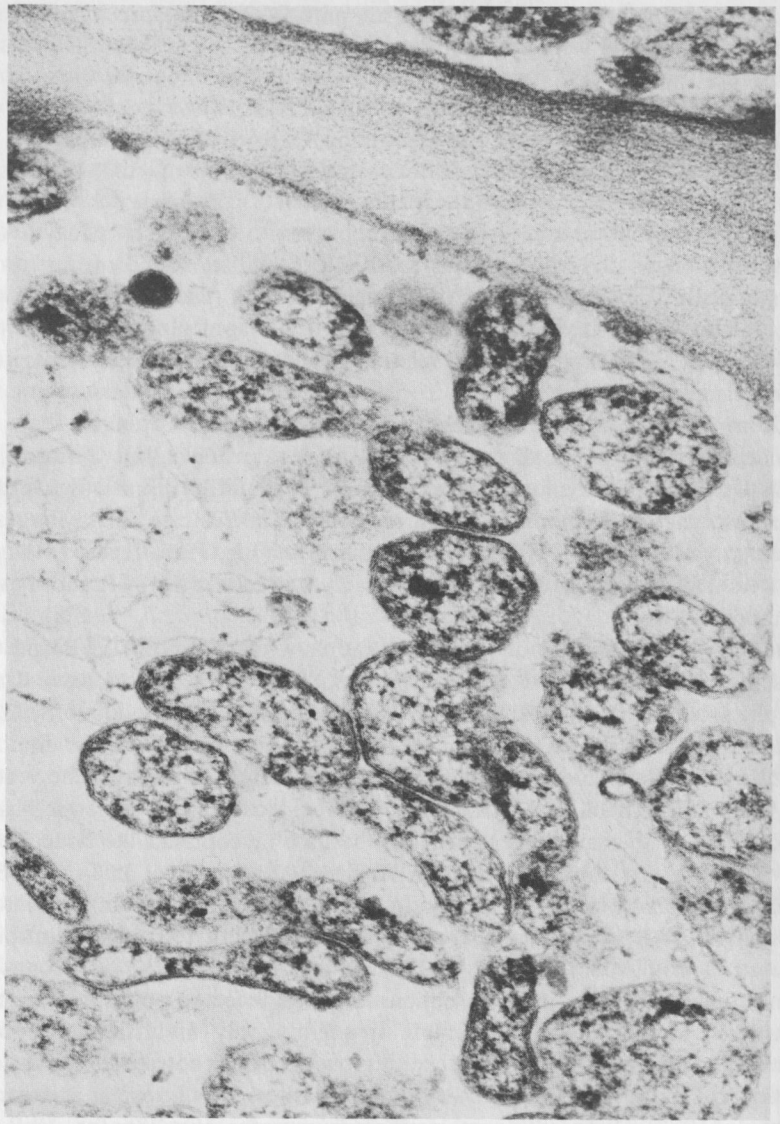


Fig. 7. Mycoplasmalike bodies in *Ribes houghtonianum* Jancz. showing yellows symptoms in flowers and fruits (J. Brčák and O. Králík, unpublished).

trap in an orchard from May 2 to October 22, 16, 219 hoppers belonging to 50 species were caught. *Macrosteles cristata* (Ribaut), *M. sexnotatus* (Fallén), and *Javesella pellucida* (Fabricius) were found most frequently. Little is known about the host range of AWB. Brčák (1974) failed to transmit the AWB agent by means of

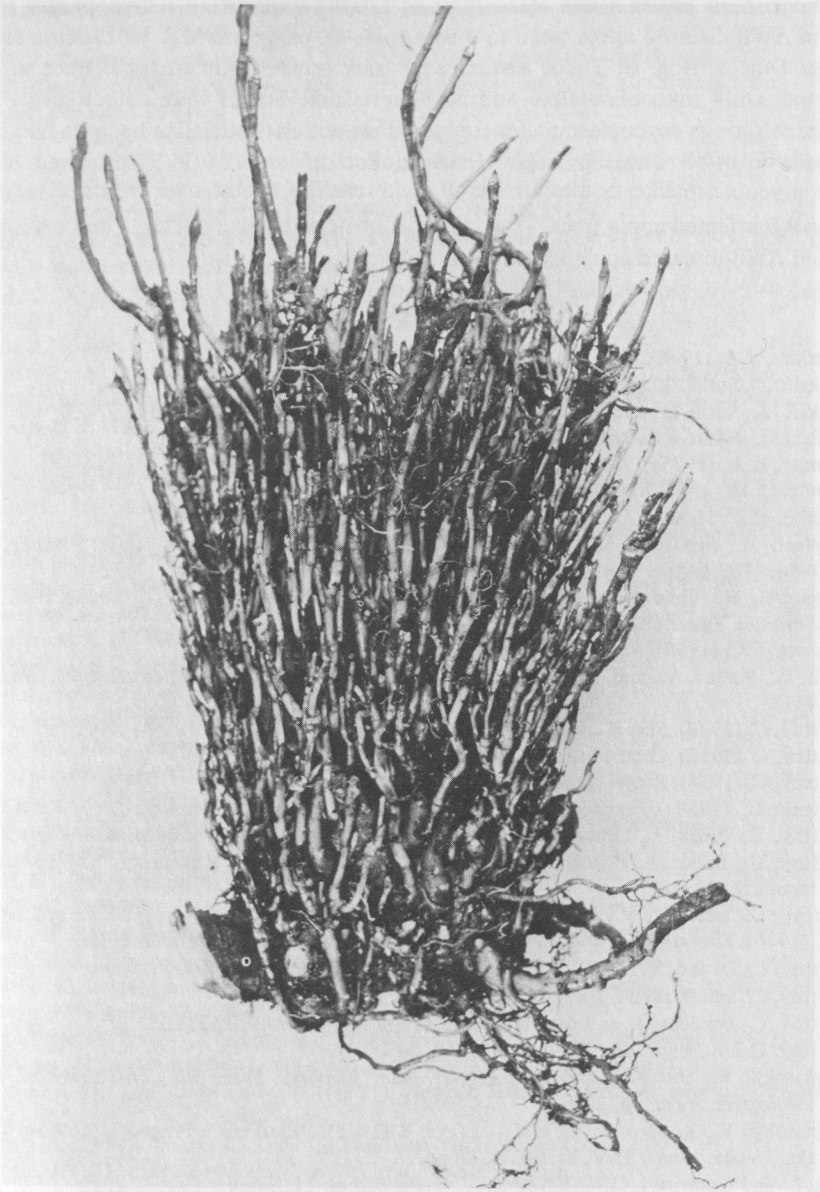


Fig. 8. Underground suckers growing from roots of an apple tree infected with the proliferation (witches' broom) disease of apples (photograph by J. Brčák).

two dodder species, *Cuscuta campestris* Yunck. and *Monogynella lehmanniana* (Bunge) Hadač & Chrtek from apple trees to apple seedlings, strawberry, tomato,

and *Nicotiana glauca* Grah. Marwitz *et al.* (1974) transmitted a mycoplasma agent from AWB-diseased apple trees to *Vinca rosea* L. using a bridge by *Cuscuta subinclusa* Dur. & Hilg. In 1976, a successful back transmission to apple trees was reported. Only mycoplasmalike and no rickettsialike bodies were detected in *Vinca rosea*, although mycoplasma alone or together with rickettsialike bacteria had been shown in AWB diseased trees. However, Petzold *et al.* (1973) observed either few mycoplasmalike bodies or many rickettsialike bacteria in ultrathin sections of AWB infected apple trees. Thus, the role of rickettsialike bacteria, and mycoplasma in AWB-diseased apple trees remains obscure.

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