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ARTHROPOD-VECTORS OF PHYTOVIRUSES IN THE RUSSIAN FAR EAST: A REVIEW

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Summary. This review presents the species diversity of arthropods-phytophages identified in the Russian Far East and capable of acting as vectors of phytoviruses. The most important taxon of these vectors is the order Hemiptera, especially the family Aphididae, whose representatives are able to transmit most of the identified phytoviruses. Viruses and their vectors are associated with host plant species cultivated in the Russian Far East: potatoes, soybeans, vegetables, and cereals.

Key words: arthropod vector, aphid, planthopper, bag, plant virus, potato, soybean, vegetable, cereal, berry.

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Резюме. В обзоре представлено видовое разнообразие членистоногих-фитофагов, выявленных на Дальнем Востоке России и способных быть переносчиками фитовирусов. Важнейшим таксоном среди переносчиков является отряд Hemiptera, особенно семейство Aphididae, представители которого способны передавать большинство выявленных фитовирусов. Вирусы и их переносчики связаны с видами растений-хозяев, выращиваемыми на Дальнем Востоке России: картофелем, соей, овощными и зерновыми культурами.

INTRODUCTION

Phytoviruses are an extensive ecological group of viruses that infect plants. The study of the ecology of phytoviruses includes an analysis of their relationships with vectors based on plant pests representing insects (Insecta) and arachnids (Arachnida) (Bragard *et al.,* 2013; Shchelkanov *et al.,* 2022). The most relevant taxon of phytovirus vectors is the order Hemiptera, among which the aphid superfamily (Aphidoidea) stands out (Dyakonov & Kakareka, 2007).

The first reports of aphids as vectors of pathogens of degradation of soybeans (Engelhardt & Mishchenko, 1931a) and rice (Engelhardt & Mishchenko, 1931b) in the Far East were made by employees of the Khabarovsk Far Eastern Regional Plant Protection Station in 1931. However, it was only after the "degeneration diseases" were mostly associated with viruses that to be transmitted by plant pests, in the 1960s, a systematic study of the ability of phytoviruses began.

A significant contribution to the research of arthropod vectors of phytoviruses on the territory of the Far East was made in the Laboratory of Virology of the Biological and Soil Institute (since 2017 the Federal Scientific Center of the East Asia Terrestrial Biodiversity) of the Far Eastern Branch of the Russian Academy of Sciences (Shchelkanov *et al.,* 2017; Shchelkanov *et al.,* 2022;). This review summarizes the data of long-term monitoring of phytoviruses and their vectors in the Russian Far East obtained by the researchers of this laboratory.

The follow abbreviations are used: AMV – alfalfa mosaic virus; BCMV – bean common mosaic virus; BYMV – barley dwarf mosaic virus; CaMV – cauliflower mosaic virus; CMV – cucumber mosaic virus; MDMV – maize dwarf mosaic virus; NCMV – northern cereal mosaic virus; PLRV – potato leafroll virus; PSTV – potato spindle tuber viroid; PVM – potato virus M; PVS – potato virus S; PVY – potato virus Y; RaMV – radish mosaic virus; ROMV – russian oat mosaic virus; RSV – rice strip virus; TuMV – turnip mosaic virus; WMV – watermelon mosaic virus.

VECTORS OF PHYTOVIRUSES ON POTATO AND SOLANACEOUS PLANTS

Cultivated plants of the Solanaceae family in the Russian Far East are represented by several species and a large variety of cultivars: tomatoes (*Lycopersicon esculentum*, *L. pimpinellifolium*), eggplant (*Solanum melongena*), pepper (*Capsicum annuum*), and potatoes (*Solanum tuberosum*). In the Far Eastern wild flora there are 6 species of the genus *Solanum* (among which 2 are native – c *S. kitagawa* and *S. megacarpum*) and introduced species of the genera *Datura*, *Lycium*, *Nicandra*, *Physaliastrum*, *Physalis*, and *Physochlaina*. Potatoes are one of the leading and most valuable food crops in the world. In connection with vegetative reproduction, the reservation and accumulation of pathogens for infectious diseases occur. Among them, viral diseases play a leading role, most of which are entomophylic (Dyakonov, 1977; Lebedeva *et al.,* 1982; Kakareka *et al.*, 2019; Volkov *et al.,* 2014; Volkov *et al*., 2019). The range of host plants for these viruses includes a significant number of wild and weedy plant species that act as natural reservoirs, from which pathogens can penetrate into agrobiocenoses (Kostin, 2005; Romanova *et al*., 2007; Volkov *et al*., 2014).

It was found that the following aphid species feed on potatoes and other solanaceous species: cotton aphid (*Aphis gossypii*), foxglove aphid (*Aulacorthum solani*), potato aphid (*Macrosiphum euphorbiae*), and green peach aphid (*Myzus persicae*), which are vectors of various viral diseases of these crops. The first winged specimens of aphids appear on potatoes in early June. Larvae and wingless individuals are absent in the mass on potato leaves, which indicates the migratory nature of settlement. Aphids fly from overwintering sites, and from intermediate forage plants. Within 5–10 days, in the absence of predators and parasites and a favorable food supply, a rapid increase in the number of insects is observed. In the conditions of the Far East, solanaceous can be populated by melon aphid (*Aphis frangulae*) and black bean aphid (*Aphis fabae*), which are also non-specific for these crops and are also capable to spread phytoviruses.

Experimental studies have shown that *M. persicae* is the most effective vector of potato and solanaceous vegetable viruses in the conditions of the Far East. In particular, PLRV is transmitted by individuals of this species with an efficiency of 80–100 % (Dyakonov, 1977), and PVS and PVM with an efficiency of 60–80 % (Dyakonov, 1976). At the same time, the degree of infection of the vector depends on the feeding time on the viral plant: 30 % of virophorous aphids acquire virus in 1 minute, and almost 100 % in 1 day. Taking into account the results of experimental studies, individuals of the Far Eastern populations of *A. solani* and *M. euphorbiae* also have a high level of virophoricity (Dyakonov *et al*. 1994). Infection with solanaceous plant viruses correlates with an increase in the number of winged aphids. The peak of morbidity is usually observed 20 days after the peak of aphid migration (Volkov *et al.,* 2019).

Accidental settlers on solanaceous plants may also be non-full-cycle species of aphids unusual for these crops when they actively move in search of more favorable food or when they are passively transported by the wind. In all cases, such aphids with virusophoric properties will perform only trial injections on cultivated plants without causing noticeable damage as direct pests but rather spreading some non-persistent and quite contagious viruses.

In terms of the abundance of species found in Solanaceae, beetles (Coleoptera) occupy second place in importance. The 28-spotted potato ladybird (*Henosepilachna vigintiocto-maculata*) has the highest harmfulness value. The experiment showed that overwintered beetles, their larvae, and young adults can carry a number of potato viruses, although not as efficiently as aphids (Sobko, 2024). At the same time, high mobility, the ability to fly long distances, and high fertility make this pest a dangerous vector of potato viruses. It is established that *H. vigintioctomaculata* is a vector of joint infection of the necrotic strains PVY and PSTV (Romanova *et al*., 2007; Shchelkanov *et al.,* 2022).

Lebedeva *et al*. (1982) indicate the tarnished bag (*Lygus pratensis*) as a vector of viruses on the solanaceous plants. Nevertheless, according to updated data, a similar species is common in the Far East the meadow bag (*Lygus rugulipennis*) and is considered to be a vector of solanaceous infecting viruses: overwintered imagoes, larvae of the 1st and 2nd generation, hatched and grown on viral potato plants, all of which can spread viruses and even preserve them since the autumn of the previous year (Lebedeva *et al*., 1982; Shchelkanov *et al.,* 2022).

VECTORS OF PHYTOVIRUSES ON NON-SOLANACEOUS VEGETABLES

Long-term ecological and virological monitoring has shown that there is a high degree of virus damage to many vegetable crops in the Far Eastern region of Russia (Tolkach *et al.,* 2019; Tolkach *et al*., 2023). Besides solanaceous crops, cruciferous crops are widespread in this region: cabbage (*Brassica* spp.), turnips (*Brassica rapa* subsp. *rapifera*), daikon (*Raphanus raphanistroides*), radish (*Raphanus sativus*), loba (*Raphanus sativus* var. *lobo*), etc.

The most dangerous pathogens for cruciferous plants are two entomophylic viruses: CaMV and TuMV. These pathogens easily infect many cruciferous species, and in winter they persist in infected mother plants and in *Brassica* spp. stumps left uncollected in the field. Natural reservoirs of CaMV are weeds from the Brassicaceae family, for example, wintercress (*Barbarea vulgaris*) and Shepherd's purse (*Capsella bursa-pastoris*). The causative agent of the disease is easily transmitted by aphids: *M. persicae* and mustard aphid (*Lipaphis erysimi*) are able to tolerate CaMV even after one short-term trial injection of a diseased plant. In contrast, cabbage aphid (*Brevicoryne brassicae*) tolerates CaMV only after prolonged feeding, but the ability to infect persists for more than 24 hours. Non-specific for plants of the Brassicaceae family, Pea aphid (*Acyrthosiphon pisum*) is also able to tolerate CaMV, but only after prolonged perception. The main types of aphid vectors in TuMV are

A. gossypii, *B. brassicae*, and *M. persicae*. Both winged and wingless forms of *A. gossypii* and *B. brassicae* can transmit this virus, and the percentage of transmission by wingless individuals is higher than by winged individuals of the same species. The period of preservation of TuMV by the aphids *M. persicae* and *A. gossypii* is longer than in other aphid species. *L. erysimi* inhabits plants of the Brassicaceae family, but its transmission of TuMV has not been identified (Bak *et al.,* 2013; Dyakonov, 1977; Dyakonov & Kakareka, 2007; Volkov *et al*., 2019; Tolkach *et al.,* 2019a; Tolkach *et al.,* 2019b; Tolkach *et al*., 2023).

RaMV identified in the southern part of Primorsky krai on the loba and radish could be transmitted by the tobacco flea (*Epitrix hirtipennis*) and the spotted cucumber beetle (*Diabrotica undecimpunctata*) both in native conditions and under the experiment (Krylov *et al.,* 1981).

Several crops from the Cucurbitaceae family grow in the south of the Russian Far East: cucumber (*Cucumis sativus*), scallops (*Cucurbita pepo* var. clypeata), zucchini (*Cucurbita pepo* var. cylindrica), pumpkin (*Cucurbita pepo* var. pepo), and less often watermelon (*Citrullus lanatus*) and melon (*Cucumis melo*). In addition to the CMV mentioned above, acidophilic WMV was found and identified on zucchini and pumpkin. In nature, aphids (mainly *M. persicae*) serve as effective vectors for WMV. Other species of aphids are also investigated to transmit WMV: the black legume aphid (*Aphis craccivora*), *A. fabae*, and *A. pisum*. The dynamics of WMV infection in the field is associated with the dynamic spread of aphids in melon crops. A high level (more than 80 %) of virus transmission by *M. persicae* was revealed in the experiments (Adlerz *et al.,* 1974; Tolkach *et al.,* 2019; Tolkach *et al.,* 2023).

VECTORS OF PHYTOVIRUSES ON LEGUMINOUS PLANTS

The primary sources of infection for cultivated plants of the Fabaceae family are seedlings grown from virus-infected seeds or natural foci. In the future, the infection spreads mechanically or with the help of insects, mainly aphids.

Since soybeans are the most common crop in the region, the study of their diseases and pests has been focused on. According to various estimates, the share of infected seeds in soybean planting materials ranges from 4–6 % up to 24 %, and the infection rate of plants at the end of the growing season is 50–98 % (Dyakonov *et al.,* 1994; Kakareka *et al.,* 2021). Such intensive infection of crops can occur only in the presence of a mass and mobile vector of the causative agent of infection. It should be noted that the vast majority of viruses affecting legumes are easily spread by insects (Volkov *et al.,* 2004; Kakareka *et al.,* 2019; Kakareka *et al.,* 2021). The entomofauna of the soybean field in the Russian Far East includes over 100 species of phytophagous insects, 20 of which cause the greatest harm to soybean crops. The proportion of aphids was up to 74 % of the total number of captured insects. An important consequence of such a variety of insects is the high level of infection of crops with viral diseases. In addition to aphids, other insect species can also be vectors for phytoviruses (Dyakonov *et al*., 2006; Shchelkanov *et al.,* 2022).

The settlement of soybeans with aphids begins at germination. In some years, it is possible to visually observe the mass movement of winged migrants of aphid *A. solani* to soybean seedlings from nearby potato fields. Numerous observations and experimental studies have established that *A. solani* in the south of the Far East can also develop as a full-cycle form with overwintering in the egg phase in the *Filipendula* plants. At the same time, *Filipendula*-migrants differ from *A. solani* morphs by only two rows of sclerotized spots on the tergites of the abdomen (Dyakonov *et al*., 2005). Among the first inhabitants of soybeans larvae and adult wingless individuals predominate almost exclusively in two species: *A. solani* and *A. gossypii*. Species of the genus *Aphis* as well as *M. persicae* and gooseberry-sowthistle aphid (*Hyperomyzus pallidus*) were less than 1 %.

The composition of aphids collected with the help of Moericke traps (Moericke, 1951) is very diverse and includes over 20 species. In addition to the already mentioned aphids, winged migrants of knot grass moth (*Acronicta rumicis*), sorrel flower aphid (*Aphis acetosae*), *A. craccivora*, apple aphid (*Aphis pomi*), carrot willow aphid (*Cavariella aegopodii*), chenopodium aphid (*Hayhurstia atriplicis*), pale green bedstrow aphid (*Hydaphias helvetica*), hemp aphid (*Phorodon japonensis*), English grain aphid (*Sitobion avenae*), etc. were detected. The most widespread type among migrants remains *M. persicae*, which accounts for over 25 % of all aphids caught in traps. It is noted that in the environmental conditions of the Russian Far East, soybeans are massively harmful to *A. solani*. However, the most widespread colonization of soybeans is carried out by soybean aphid (*Aphis glycines*) (Dyakonov, 1973), although this species does not winter in the Russian Far East and migrates to Russia from neighboring provinces of China, as confirmed by Chinese researchers (Wang & Ghabrial, 2002; Wu *et al.,* 2004; Zhang, 1988). To a certain extent, this explains the unexpected appearance of *A. glycines* in significant numbers in the soybean fields of Primorsky krai during the second half of July. The abnormally high number of this species, shown as a result of direct calculations, and the fact that in just a week (per generation), the population density increases 5–7 times indicate a high degree of migration of this species of aphids. It is migration of *A. glycines* that explains the peak in the number of aphids on soybeans in late July-early August (Dyakonov *et al*., 2006; Volkov *et al.,* 2019).

Wild plants of the genera *Melilotus*, *Trifolium*, and *Vicia* are a source of aphidophylic viruses – AMV, BCMV, BYMV, and CMV – which can be spread by a wide range of aphid species among cultivated legumes (Kostin, 2005).

VECTORS OF PHYTOVIRUSES ON CEREAL PLANTS

Among grain cereals (Poaceae) in the Russian Far East, there are common wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), and rye (*Secale cereale*); paniculate cereals: oat (*Avena sativa*), rice (*Oryza sativa*), millet (*Panicum miliaceum*), foxtail millet (*Setaria italica* subsp. *italica*), sorghum (*Sorghum nervosum*), and maize (*Zea mays*).

Small brown planthopper (*Laodelphax striatellus*), wheat curl mites (*Aceria tosichella*), and several species of aphids: corn leaf aphid (*Rhopalosiphum maidis*), bird cherry-oat aphid (*Rh. padi*), wheat aphid (*Schizaphis graminum*), and *S. avenae* cause the greatest harm as vectors of cereal viruses in the Russian Far East. About 20 species of aphids are direct colonizers and pests of grain crops (including rice) in Primorsky krai: Dogwood aphid (*Anoecia corni*), Wheat-barley aphid (*Anoecia vagans*), Spindle-tree (*Aphis evonymi*), Pistachio-grass root aphid (*Forda formicaria*), Pistachio-leaf wrinkling aphid (*Forda hirsuta*), Root collar aphid (*Forda marginata*), Eastern aphid (*Forda orientalis*), Mealy plum aphid (*Hyalopterus pruni*), Mackauer aphid (*Iziphya mackaueri*), Rose-grain aphid (*Metopolophium dirhodum*), Apple-grass aphid (*Rhopalosiphum insertum*), Honeysuckle-grass aphid (*Rhopalosiphum lonicerae*), *Rh. maidis*, Waterlily aphid (*Rhopalosiphum nymphaeae*), Bird cherry-oat aphid (*Rhopalosiphum padi*), *Schizaphis graminum*, Oriental pear aphid (*Schizaphis piricola*), Bristly olive grass aphid (*Sipha elegans*), *S. avenae*, Elm sack gall aphid (*Tetraneura ulmi*). Most of them are parasitic on the roots. As mentioned above, four species of aphids dominate the cultivated cereals: *Rh. maidis*, *Rh. padi*, *S. avenae*, and *Sch. graminum*. Aphid-polyphages – *M. persicae*, *B. brassicae*, *A. gossypii*, *A. craccivora* – accidentally fall on plants of cereal fields and rice developing mainly on other forage plants. All of the above aphid species can transmit BYDV and MDMV, which exacerbates their harmfulness (Pashchenko, 1979; Mamaev, 1996; Dyakonov & Sapotskiy, 2004; Kakareka *et al.,* 2020; Volkov *et al*., 2024).

NCMV is one of the most harmful entomophilic viruses and is spread by *L. striatellus*. The complex nature of the relationship between cicadas and plant communities is reflected in the transmission of this virus. NCMV reproduces directly in the vector, making the infected individual a permanent (up to death) source of infection, which can infect a large number of plants, taking into account a high level of *L. striatellus* mobility. This pathogen overwinters in infected larvae (Mamaev, 1996).

On the territory of Primorsky krai *L. striatellus* is also a vector of two tenuiviruses: ROMV and RSV. They can be transmitted transovarially, therefore a certain part of the eggs affected by females is infected with this virus, and the hatched larva can infect plants during feeding. The rice leaf beetle (*Oulema oryzae*) also appears to be the vector for RSV in the south of the Russian Far East (Lebedeva *et al*., 1982; Kakareka *et al*., 2020; Volkov *et al*., 2024). Here, only two cereal viruses transmitted by aphids have been identified: BYDV and MDMV. The range of aphid vectors for BYDV includes about 15–20 mass species of the Far Eastern aphidofauna (Dyakonov & Sapotskiy, 2004; Kakareka *et al*., 2020).

VECTORS OF PHYTOVIRUSES ON GARDEN AND BERRY CROPS

Several viruses from the genus *Nepovirus* have been identified on berry crops in Primorsky krai, many of which are spread by root nematodes from the genera *Xiphinema* and *Longidorus*. However, TRSV can also be spread by aphids (Dyakonov, 1976; Kakareka *et al.,* 2017). In populations of wild berries–Manchurian currant (*Ribes mandshuricum*), Korean raspberry (*Rubus crataegifolius*), Sakhalin raspberry (*Rubus sachalinensis*), and Siberian mountain ash (*Sorbus sambucifolia*) a significant number of still unidentified viruses were described (Kostin, 2005; Volkov, 2022).

Acyrthosiphon spp., waxy honeysuckle aphid (*Amphicercidus japonicus*), large blackberry aphid (*Amphorophora rubi*), gooseberry aphid (*Aphis grossulariae*), small raspberry (*Aphis idaei*), *A. pomi*, small bramble aphid (*Aphis ruborum*), leaf curling plum aphid (*Brachycaudus helichrysi*), red currant (*Cryptomyzus ribis*), hawthorn-carrot aphid (*Dysaphis crataegi*), oriental apple aphid (*Dysaphis orientalis*), Far Eastern apple aphid (*Hyalomyzus malisuctus*), *H. pruni*, blackcurrant-sowthistle aphid (*Hyperomyzus lactucae*), *H. pallidus*, barberry aphid (*Liosomaphis berberidis*), rose aphid (*Macrosiphum rosae*), *M. dirhodum*, Lesser rose aphid (*Myzaphis rosarum*), blackberry-grass aphid (*Sitobion fragariae*) have been identified on fruit and berry crops in the Russian Far East. For many of the listed aphid species, the ability to transmit entomophylic viruses has been shown (Martin *et al.,* 2013; Martin & Tzanetakis, 2013).

ECOLOGICAL PECULIARITIES OF PHYTOVIRUSES AND THEIR VECTORS IN THE RUSSIAN FAR EAST

At first glance, it may seem that perennial woody and shrubby plants (primary forage plants for full–cycle aphids) for the most part are long-term reservoirs of some viruses (CMV, AMV, BYMV, PVS, PVY) that infect field and garden crops and that fruit and tree plantations are a kind of anthropogenic focus of aphid-vectors for phytoviruses. In fact, these relationships are not as binding as they may seem. Firstly, migratory species of aphids use trees and shrubs (including fruit and berries) as their main food plant for a short time only the first 2–3 generations. Individuals hatched from overwintered eggs are intact for viruses. In the process of feeding, aphids can only perceive viruses specific to the listed plants. Secondly, infection of trees and shrubs with viruses having a very wide range of host plants (CMV, AMV, etc.) can occur in only two cases: in case of accidental visits by incomplete aphid species of similar plants and when remigrating to them from herbaceous plants of full-cycle aphid species. But in both cases, aphids must be virusophoric, that is, they carry viral particles on a stiletto. The flight time of the vector from virulent herbaceous plants to woody and shrubby plantations should be limited so that the vector does not have time to lose its infectivity. A full-cycle species of aphids returns to the main forage plant to lay eggs and no longer feed on it.

But, generally speaking, infection of woody and shrubby plants with entomophilic viruses having a very wide range of host plants is possible, especially if the acceptor plant is in the seedling stage. This is evidenced by both experimental data and the results of visual observations. For example, after epiphytotic CMV in one of the nurseries in Primorsky krai this virus was detected on the juvenile apricot (*Armeniaca mandshurica*) trees (Keldysh & Pomazkov, 1985; Volkov *et al*., 2022).

The epiphytology of viruses detected on vegetable and melon crops is closely related to the agrotechniques of these plants, the presence of sources of infection, and the passage of the stages of the vector life cycle. In this regard, an important factor in the development of infections caused by entomophilic viruses is the location and dynamics of aphid reproduction. The interactions in the "virus-vector-host" system in the environmental conditions of the Russian Far East differ from those in other regions. It was shown that there are no aphids on greenhouse plants in the southern regions of Primorsky krai. This is probably due to the fact that during the period of seedling distillation, full-cycle dioecious aphids have not yet completed their development and reproduction on primary host plants. Due to the relatively low air temperature, there is also no spread of incomplete cyclical aphids from their overwintering sites (greenhouses, living quarters, vegetable storages, and potato storages). Thus, aphids get the virus later. An abundant food supply leads to the rapid reproduction of aphids. The degree of aphid colonization of plants grown for commercial purposes and for seeds can reach 20–30 %, therefore, they cause damage as pests reducing yields and worsening the presentation of products.

In the presence of primary sources of entomophylic viruses, plants become infected very quickly. Therefore, the fight against aphids becomes important at the earliest stages of the distillation of vegetable seedlings. In addition, aphids are an active vector of viruses that have accumulated in greenhouses and in natural communities forming secondary foci of infection.

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