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RESEARCH ARTICLE

Invasive insect pests of introduced plants of the “Olexandria” Dendrological Park. Report 3: towards a biology of *Pineus orientalis* (Dreyfus, 1889) (Heteroptera: Adelgidae)

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Abstract

The article discusses problems associated with the introduction of plants and the accompanying invasion of new species of insect pests into park plantings. It emphasises the urgent need to study their biology. The paper describes some biological features of one of the invasive species of pests – the Eastern pine adelgid, *Pineus orientalis*. The data on phenology, feeding and reproductive features, number of generations, composition of life cycle morphs, and damage caused by *P. orientalis* to its forage plants are presented.

Keywords: *Pineus orientalis*, plant introduction, biological invasions, full development cycle, side development cycle, diapause, life cycle morphs

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Introduction

The study of pests and diseases of introduced plants is integral part of scientific research aimed at solving, among other things, such problems as, assessing the pressure of the new biotic environment on the introduced plant, the impact of introductions on local ecosystems due to the introduction of new pests and pathogens, a detailed study of the biology of invading pests, organization of the monitoring and ways to manage their numbers. All the issues are related to a more general problem – the problem of biological invasions. Currently, this topic has become a central theme in modern ecological and

environmental research (Ehrenfeld, 2010; Strayer, 2012; Carneiro et al., 2024).

Biological invasions are one of the main components of today’s global changes. Through mechanisms such as predation, hybridization, or competition, invasive species offer unique opportunities to understand fundamental evolutionary and ecological processes, thanks to their ability to adapt to new environments and successfully compete with native species (Haubrock et al., 2023).

The “Olexandria” State Dendrological Park of the National Academy of Science of Ukraine (Dendropark “Olexandria”), located in the Kyiv region (Ukraine), has also faced the problem of biological invasions. The natural conditions

and terrain of the park are conducive to the growth and development of a diverse range of vegetation. Nearly 1,200 species and forms of tree species from various floristic zones worldwide grow in the park (Boyko et al., 2013).

One of the consequences of the large-scale introduction of plants into the park was the invasion of new species of tree-eating insects into its plantings. Over the past twenty years, the park's entomofauna has been enriched by at least 20 species of insect invaders (Dragan & Dragan, 2024), and this list continues to grow. In 2025 alone, about 36 such species have already been identified. Park ecosystems saturated with introduced plants have proven to be highly favorable for the establishment of invasions and the formation of stable populations. An example of successful insect invasions in park plantings is the plane tree leaf miner (*Phyllonorycter platani* Staudinger, 1870), which has been severely damaging a group of plane trees in the Great Meadow landscape area for several years, or the Japanese lime leaf miner (*Phyllonorycter issikii* Kumata, 1963), which has been found en masse on many species of *Tilia* spp. Another invasive species, the oak lace bug (*Corythucha arcuata* Say, 1832), also poses a great danger to park plantings. Currently, it damages introduced oak species, such as *Quercus macranthera* Fisch. & C.A.Mey ex Hohen, *Q. castaneifolia* C.A.Mey, *Q. serrata* Murray. However, *C. arcuata* causes the most damage to the local species – *Q. robur* L.

A special place among new invasive pests belongs to a group of insects from the family Adelgidae (Heteroptera). This family comprises approximately 70 species known today, which are distributed worldwide (Favret et al., 2015; Havill et al., 2025). Among them are many serious forest pests (Havill & Foottit, 2007). These include, in particular, the eastern pine adelgid, *Pineus orientalis* (Dreyfus, 1889), which comes from Western Caucasus and Anatolia (Turkey). In this area, its primary host, the Eastern spruce (*Picea orientalis* (L.) Link), and local pine species (secondary host plants) naturally grow. In Europe, *Pineus orientalis* is widespread almost everywhere in parks where its forage plants are found (Steffan, 1972; Liska et al., 2011; Albrecht, 2017).

In Ukraine, it can be found in the parks of the Forest-Steppe and Chernihiv Polissya, as well as botanical gardens of all natural zones

(Dmitriev, 1987; Dragan, 2013; Pokhilchenko et al., 2020).

Adelgids (Heteroptera, Adelgidae) have very complex life cycles. Famous researcher of this group of insects, Eichhorn (1989), noted that the development cycles of adelgids belong to the most fascinating phenomena in biology, and their progressive understanding is one of the remarkable achievements of entomologists. Despite a long history of studying their life cycles, many questions concerning the general biology of adelgids, as well as the specific biology of individual species, remain insufficiently studied. One such species is the Eastern pine adelgid (*Pineus orientalis*), the biology of which has been studied for over 130 years.

According to Kholodkovsky (1915), the species was first described by Dreyfus in 1888 on Eastern spruce, where it produced long spindle-shaped galls. Marshal (1913) considered this species to be the eastern race of the European *Pineus pini* Macq. Kholodkovsky (1915) suggested that *Pineus pini* and *P. orientalis* were originally one indigenous southern species, which then split into two: one southern (*Chermes* (= *Pineus*) *orientalis* sensu stricto) and one northern (*Ch. pini*), which lost the ability to form galls and retained migration only as a biological rudiment. According to modern studies employing the molecular methods (DNA barcoding), the *Pineus pini* / *P. orientalis* species complex is essentially a single species (Havelka et al., 2019).

Steffan (1972) classified this adelgid as a typical holocyclic species with five generations (fundatrix, alata migrans, hiemosistens, sexupara = andropara + gynopara, and sexualis), the order of which is genetically determined (Fig. 1).

Some recent authors also describe the five-generation complete life cycle of adelgids as typical (Havill & Foottit, 2007; Sano & Ozaki, 2012).

Lampel (1968), considering adelgids in general, also pointed out that their complete life cycle consists of five stages. In this case, each morph within the main cycle is usually represented by one generation, and before sexupara, there is only one generation of settlers. However, referring to the works of other authors (Böerner & Heinze, 1957), he considered the Eastern pine adelgid to be

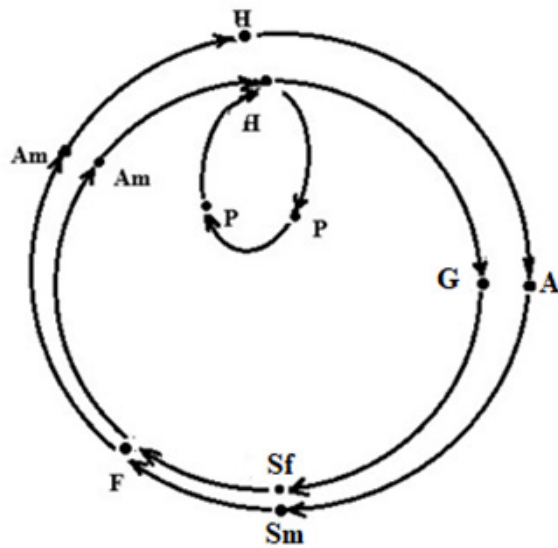


Figure 1. Diagram of the life cycle of the Eastern pine adelgid (*Pineus orientalis* Dreyfus, 1889) adapted from Steffan (1972). Designations: F - fundatrix; Am - alata migrans; H - hiemosistens; P - progrediens; A - andropara; G - gynopara; Sm - males; Sf - normal females.

an exception, since this species has two or three generations of settlers before sexupara. Later, Liska et al. (2011) proposed a schema for the development of *Pineus orientalis* that was significantly different from the others. This schema included winged form of the settlers (i.e., alata exsulans, according to the generally accepted terminology for adelgids) as well as several generations of sistentes (Liska et al., 2011). The existence of the *Pinus orientalis* morph sistens in the life cycle is also mentioned in other sources (Dransfield & Brightwell, 2025).

According to the concept of double cycles (Steffan, 1968, 1972), the life cycle of the Eastern pine adelgid consists of two parallel phases, male and female, which interact only during the sexual reproduction of the amphigonous generation. At the same time, a secondary developmental cycle (paracycle) is assumed only in the female line. Consequently, with the temporary loss of the primary host, the adelgid population loses the potential opportunity to restore the holocycle due to the loss of the ability to produce androparous and male forms. It should be noted that this concept was later emphasized (Eichhorn, 1989; Alles, 1994), and the limits of its applicability to the entire group of adelgids remain unknown.

Several other issues important for understanding its biology also remain unclear. Meanwhile, to the best of our knowledge, there is very little research on this issue. This article presents the results of studies that complement and clarify the existing knowledge about the life cycle of *Pineus orientalis*.

Material and methods

All stationary observations and experiments were carried out in the Dendropark “Olexandria” in 1998–2024. Seedlings of pine (*Pinus sylvestris* L.) in containers were used to study the peculiarities of the seasonal development of *Pineus orientalis*. All experimental pine plants were free from settlement by any phytophagous insects that could affect the course and results of the research.

Non-opened pine adelgid galls were transferred to experimental pine seedlings. The nymphs emerging from galls molted into adult winged females. These females moved to the needles of pine trees and began to lay eggs there. Larvae hatched from the eggs, which fed on the bark of shoots and developed there into imagoes. The egg clutches of these adults were transferred to uninfected plants. This procedure was then repeated until the end of the season. The last generation of the year did not develop into imagoes and instead entered winter diapause in the larval phase at various ages. Three years after the experiment began, the experimental pine plants with adelgid colonies were transferred to a site where Eastern spruce trees (*Picea orientalis*) had been growing for many years. During the entire previous period, no damage (galls) by any species of adelgids was ever recorded on them. Since this procedure was carried out in early spring, the appearance of winged sexupara flying from experimental plants was observed on the Eastern spruce in the same year, and galls of a typical form were observed the following year.

The preparation of microslides was carried out according to the generally accepted method in aphidology (washing in alcohol, maceration of soft tissues in a KOH solution, mounting in Fora liquid). Photos were taken using the built-in camera on the Oppo Reno 8 T smartphone.



Figure 2. First instar larval skin of *Pineus orientalis*. × 200.



Figure 3. Adult fundatrices – white waxy lumps at the base of spruce (*Picea orientalis*) needles.

Results

According to the results obtained, the seasonal development of *Pineus orientalis* is as follows. On the Eastern spruce, the first-age fundatrix larvae (Fig. 2) overwinter, attached to the bases of the needles on the shoots of the last year of life.

The spring reactivation of overwintering larvae was observed in different years depending on weather conditions from the end of March to the second decade of April. After three molts, they turn into adult parthenogenetic females, which reproduce within a few weeks, laying up to 200 eggs (Fig. 3).

The alata migrans larvae hatching from them move to the bases of the needles on the green shoots of the current year. Under the influence of their sucking, the bases of the needles, and often the adjacent part of the stem, swell, forming chambers in which the larvae feed and develop into nymphs (larvae of the last fourth instar). The galls of the Eastern pine adelgid (Fig. 4) are pretty diverse in shape. Most often, these are spindle-shaped neoplasms of various but sometimes slightly shortened and curved shoots, in which all or almost all needles swell at the base. The shape of the galls is apparently determined by the state of the shoots at the beginning of their

settlement by the phytophagous larvae. Spruce shoots at an early stage of their development are more sensitive to the effects of growth-active substances released by the larvae during sucking. Hence, the more profound transformations of the shoot. In other cases, when the shoot completes its normal development, the invasion of the larvae only slightly transforms it.

The opening of the galls of *Pineus orientalis* was observed in some years as early as the end of May, but in other years, it occurred during June. Migration to pine begins, as a rule, in the second decade of June and ends by the 1st decade of July. Migrants lay up to 25–30 eggs on pine needles. After 10–15 days, larvae hatch from them, which feed on the bark of shoots of different ages or very rarely on needles. During heavy precipitation, the latter are most often washed away by rain.

After four molts, these larvae mature into parthenogenetic egg-laying females, giving rise to three or four generations of settlers. It should be emphasized that all individuals of settlers, developing on a secondary host, without exception, reach maturity after passing four larval instars.

Morphologically, individuals developing on pine throughout the season are very similar, although there are some differences of a purely quantitative nature. The differences



Figure 4. *Pineus orientalis* on *Picea orientalis* shoots: **A** – galls on young shoots; **B** – damage to shoots remaining after galls dry up.

concern the size of the body, the degree of its sclerotization, and the number of wax glands (Fig. 5).

External factors determine the transition to winter diapause, with the most significant ones being the reduction of photoperiod, the condition of the food plant, and a decrease in temperature. In warm, humid, and prolonged autumn seasons, the onset of diapause in settlers shifts from the usual end of September to the beginning of October, and then to the end of October, to the start of November. Larvae of all four ages overwinter on pine, but mainly larvae of older ages, and, as a rule, the last two generations of the year.

The spring resumption of the development of overwintered larvae is closely related to the beginning of vegetation (bud swelling) in pine. The first reactivated larvae can be observed, depending on weather conditions, from the second half of March to the second decade of April. Transformation into adult parthenogenetic females occurs after a total of four molts. Individuals that overwintered in older larval instars in the imago phase have larger sizes, a greater degree of sclerotization, and waxy pubescence of the body than individuals that went into winter

diapause as larvae of the first or second instar.

The mass maturation of the overwintering generation typically occurs at the end of April. Still, in years with an early and warm spring, it may occur at the beginning of this month. Females lay eggs, 70–110 in total, over two and a half to four weeks. From these, larvae of the next (first summer) generation emerge, which primarily move to May shoots of pine. However, some of them populate the bases of needles under the film covering, the bark of shoots from previous years of life, thick branches, and even the trunks of young pine plants. After a little less than a month, they turn into either wingless or winged adult females.

Wingless females of the first summer generation give rise to several more generations of the same individuals. In total, up to six summer generations of settlers can develop on a pine within the paracycle during the season.

The appearance of the winged females (sexupara) varies slightly by year. Thus, over a long-term observation period, we noted a difference of only a few days (May 18–22). In nature, the winged females always develop only on young May shoots. In experimental conditions (complete removal of growth buds

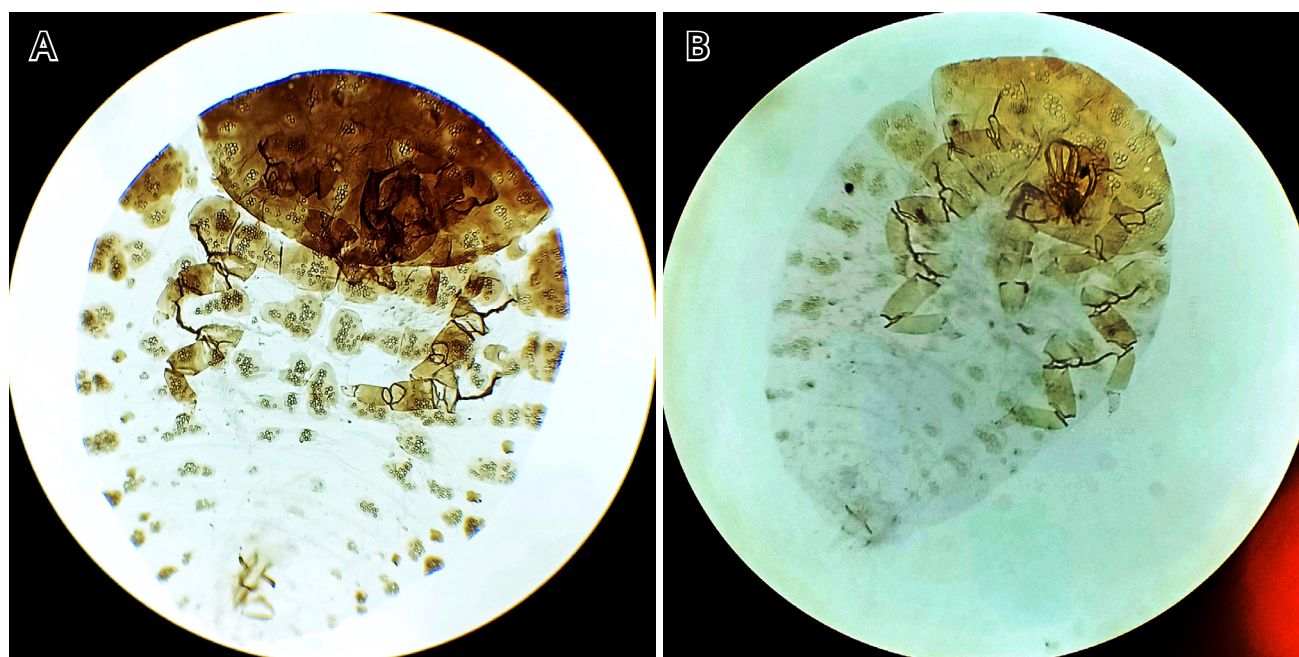


Figure 5. *Pineus orientalis*: **A** – adult hiemoprogressus; **B** – adult aestivoprogressus. $\times 80$.

in spring), they also occurred on needles. No other winged forms develop on the pine except for the sexupara. The report of alata exsultantes in the life cycle of *Pineus orientalis* (Liska et al., 2011) has not been confirmed in our research.

As our studies have shown, sexupara *Pineus orientalis* remigrate to the primary host with immature sexual products and therefore need additional nutrition. As a result, they lay eggs for one to two weeks. In this case, a relatively small number of eggs are laid – up to 20 pcs.

As a result of the sexupara sucking on the spruce needles, the latter turns yellow and is slightly deformed. When feeding, females produce abundant waxy pubescence (Fig. 6). Under the protection of this pubescence and the wings of the female itself, the development of the next generation occurs – sexual females and males. In this case, the sexupara – gynopara and andropara, produce individuals of one sexual type – either females or males.

The maturation of individuals in the sexual generation – specifically, normal females and males – occurs during July and early August. As a result, copulation and laying of fertilized eggs by normal females is also stretched out in time. After fertilization, females climb into various secluded places, often these are the remains of scales between annual growths, where they lay only one egg. From them, fundatrix develops during July – mid-August.

This marks the end of the full two-year development cycle of the Eastern pine adelgid.

An important area of our research was the study of the peculiarities of the Eastern pine adelgid life cycle under conditions of isolation from its primary host and after restoration of this connection. Studies have shown that under isolation conditions, the development of adelgids on pine has not undergone any changes in the number of generations or in the composition of morphs. What is important to note is that every year, the adelgid colonies on the experimental plants produced winged individuals in the spring. After reconnection of communication with the primary host, the same year, the sexuparas were observed to remigrate to spruce and subsequently develop normal females and males, followed by fundatrices. The following year, galls typical of the eastern adelgid developed on the spruce. Thus, this experiment showed that the complete development cycle of this species can be restored from a paracycle that functioned for some time in isolation from it.

Discussion

The data we obtained show that the complete life cycle of the Eastern pine adelgid differs from the ‘classical’ scheme, which typically involves five generations. In total, the complete



Figure 6. *Pineus orientalis* on *Picea orientalis* shoots: **A** – galls and sexupara on the shoot tips; **B** – sexupara and damaged (dechromated) spruce needles.

two-year life cycle of this species consists of nine to ten complete generations (Fig. 7). Within the paracycle, up to six complete generations of settlers can develop on the pine tree. It can be said that the number of generations within both the holocycle and paracycle of the Eastern pine adelgid is not fixed. The data obtained generally confirm the results of Böerner & Heinze (1957), specifying, however, that after migration to the pine tree, this species can develop twice as many generations of settlers before the appearance of sexupara as these researchers indicated.

There is a widespread opinion that adelgids undergo a typical five-generation complete life cycle (Lampel, 1968; Steffan, 1972; Havill & Foottit, 2007; Sano & Ozaki, 2012). Only a few cases of deviation from this rule were reported (Lampel, 1968). However, holocycle comprising more than five generations occurs in *Dreyfusia prelli*, *D. merkeri*, *Adelges laricis* (Eichhorn, 1957, 1994), *Pineus orientalis* (Böerner & Heinze, 1957), *Dreyfusia nordmanniana*, *Aphrastasia pectinatae* (Dragan, 1996, 1999), and possibly in *Gilletteella cooleyi* (Dragan, 2012). Therefore, we do not share the opinion that a five-generation full life cycle is typical for adelgids, as suggested by some authors (Steffan, 1972; Havill & Foottit, 2007; Sano & Ozaki, 2012). On

the contrary, the data we have indicate that the five-membered holocycle of adelgid is most likely an exception with a limiting case of reduction in the number of generations in the holocycle. According to our data, a similar holocycle is present in *Sacchiphantes viridis* Ratz. and, possibly, in some other species of adelgid.

As the present studies have shown, in the Eastern pine adelgid, the development of the population on the secondary host within the holocycle proceeds synchronously with the paracyclic one. It should be assumed that such a feature is also characteristic of other adelgid species. Knowing how the adelgid population develops in the secondary cycle, it is possible to predict that the part of the population that is involved in the full development cycle will behave similarly on the secondary host.

Regarding the morphs of the Eastern pine adelgid's life cycle, in addition to the three on the primary host, there are only two on the secondary host: progrediens and sexupara (also known as andropara/gynopara).

The morph sistens, the presence of which was previously reported by other sources, is absent from the life cycle of this species. Let us clarify our position on this issue. The term 'sistens', denoting individuals developing

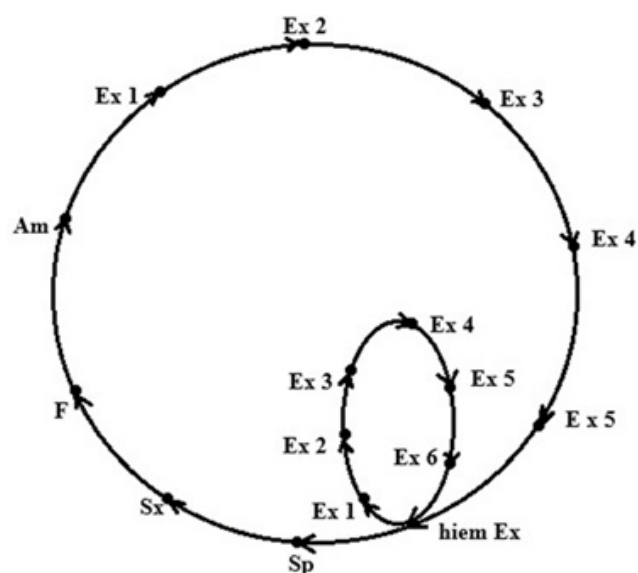


Figure 7. Diagram of the life cycle of the *Pineus orientalis* by G. Dragan (first published here). Designations: F – fundatrix; Am – alata migrans; Ex1–6 – generations of settlers (exules, progrediens); hiem Ex – hiemoprogredientes; Sp – sexupara (andropara + gynopara); Sx – sexualis (males and normal females).

on the secondary host with a period of rest, was introduced by Marshall (1913), and cited by Lampel (1968). Among them, he distinguished sistens, which develop with a break for summer diapause – aestivosistens – and those for winter – hiemosistens. He gave the name ‘progrediens’ to individuals developing on the secondary host without diapause. Steffan (1968) held similar views. He believed that the progrediens morph is unspecialized and has four larval instars, while in fundatrix, hiemosistens, and aestivosistens, the number of instars was reduced to three during evolution. In the diagram of the life cycle of *Pineus orientalis* proposed by Steffan (1968, 1972), it is clearly seen that in this species, it is precisely the specialized form hiemosistens that develops on the secondary host in three instars. At the same time, Steffan (1972) noted that fourth instar larvae can also overwinter on the secondary host, which, in connection with this, cannot be classified as hiemosistens. This contradiction does not allow us to state with certainty what views the author adhered to regarding the existence of a specialized winter-diapausing morph in the Eastern pine adelgid.

In turn, Lampel (1968) divided the individuals developing in summer on a secondary host (aestivales) into aestivoprogrediens and aestivosistens. As can be seen from the names, the former develop without diapause and the latter with diapause. He assumed that progrediens are always only aestivales, i.e., individuals that develop into adults in summer. He classified all hibernating individuals as hiemosistens (= hiemalis).

In our opinion, the assignment of wingless settlers to one or another morph should be based on biological basis rather than on seasonality. These biological characters, which allow differentiating the wingless settlers into morphs, are the number of larval instars and the presence of an obligatory diapause in the first larval instar. The latter factor is independent of external conditions and is genetically determined. All settlers of *Pineus orientalis* that winter on pine, without exception, develop into adults after four larval instars, and none of them exhibit obligatory diapause in the first larval instar. As already mentioned, their diapause is determined by external conditions, and they go to hibernation in one to four instars.

Thus, the Eastern pine adelgid generally lacks the hiemosistens morph and sistens morph in its life cycle. In fact, in this species, the non-specialized progrediens is the hibernating morph. Individuals of this morph develop without diapause in the summer season. However, with the onset of the unfavorable winter season, they enter diapause at a certain age, when the effect of external factors that eventually cause diapause reaches a critical value. We will distinguish two seasonal variations of the morphs progrediens – aestivo- and hiemoprogrediens in the eastern pine adelgid. Then, all breeding individuals of the settlers in the summer period should be referred to as aestivoprogrediens, and those breeding after winter diapause – to hiemoprogrediens. A similar approach to distinguishing between summer and winter settlers on pine was applied earlier by Annand (1928). It is the external conditions (lower temperature, shorter daylight hours) affecting the development of larvae for a sufficient amount of time in the period preceding diapause that cause the corresponding morphological changes and the characteristic appearance of ‘typical’ hiemoprogrediens. The

larvae of progrediens, whose development before diapause was short, did not exhibit corresponding morphological features in the adult phase.

However, both the former and the latter should be classified as hiemoprogressiens based on the presence of winter diapause in their development and the existence of undeniable physiological differences with aestivoprogressiens associated with their adaptation to unfavorable living conditions during the autumn-winter season.

The restoration of the full developmental cycle of Eastern pine adelgid from the paracycle after a three-year absence of the primary host apparently indicates that not only female individuals but also male ones reproduce in the paracycle. This means that the population isolated from the primary host retains for some time the potential to repopulate it in the future. It is unknown how long this possibility remains. Suppose we assume that *Pineus orientalis* and *P. pini* are one species (Havelka et al., 2019) and consider them as different races. In that case, *P. pini* is a race that, as a result of very long isolation from the primary host, has lost the male developmental cycle. This means that the time during which the holocycle can be restored is finite.

As the research has revealed, the damage caused by the pine adelgid to its primary host is due, firstly, to gall formation, which usually kills the damaged shoots, and secondly, to the sucking of the female sexparas and their offspring on the pine needles, causing them to turn yellow and partially die. The direct negative impact of the pest on the primary host is limited to the first half of the season. The nature of the damage caused by the pine adelgid to the secondary host, the pine tree, is determined by the fact that the pest reproduces and feeds on it continuously, without diapause, throughout the season. During this period, up to six generations of settlers develop in the secondary cycle. The harmfulness of these generations is not the same. The overwintering and first summer generations cause the most tremendous damage to pine trees. Densely populated by settlers, young pine shoots may dry out, or their growth may be significantly reduced, and their needles may become smaller. Subsequently, because of the remigration of a

significant part of the first summer generation to spruce, the load on young shoots decreases naturally. Precipitation (rain), which partially washes away the adelgids, as well as the activity of entomophages, also play a particular role in reducing the number of adelgids. In the summer, the presence of the pest on pine trees becomes less noticeable due to its secretive location on the plant and limited feeding activity. This is reflected in a decrease in the size and fertility of parthenogenetic females in the second and subsequent summer generations. Only in autumn is there a second (after spring) peak in the activity of *Pineus orientalis* on pine trees: the size and fertility of reproducing females increase, as does the amount of wax they produce.

Another significant result of the work done is the experimental confirmation of the impossibility of breaking the complete life cycle of adelgids due to the temporary isolation of the paracycle from the main development cycle. In practical terms, this means that planting eastern spruce in a habitat populated by adelgids that develop only in a secondary cycle on pine trees will inevitably lead to its colonization by this pest.

Based on the data obtained, the following practical conclusions can be drawn: planning of protective measures against *Pineus orientalis* should be timed to coincide with the spring period on both pest-hosting plants and in the secondary host in the fall.

Conclusions

It was found that the full life cycle of *Pineus orientalis* is not fixed and consists of nine to ten complete generations. In the paracycle, *P. orientalis* develops up to six complete generations in the secondary host.

It has been established that this species lacks a specialized neotenic winter diapausing form of sistentes on the secondary host. All wingless settlers belong to one morph – progredientes. The winter diapause in pine is facultative and is not genetically programmed. Individuals on the second host, whether winter or summer, are biologically identical and differ from each other only in quantitative characteristics: the size and degree of sclerotization of the body, as well as the number of wax glands on it.

The life cycle of *P. orientalis* lacks the winged form of settlers (*alatae exsulantes*). The sexupara of this species, unlike other species, feeds on spruce conifers before laying eggs.

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Інвазійні комахи-шкідники інтродукованих рослин дендрологічного парку "Олександрія" НАН України. Повідомлення 3: щодо біології *Pineus orientalis* (Dreyfus, 1889) (Heteroptera: Adelgidae)

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У статті розглядаються проблеми, пов'язані з інтродукцією рослин та супутнім вторгненням нових видів комах-шкідників у паркові насадження. Підкреслюється нагальна необхідність вивчення їхньої біології. В статті описано деякі біологічні особливості одного з інвазійних видів – східного соснового хермеса (*Pineus orientalis*). Вперше представлені дані про фенологію, особливості харчування і розмноження, числу генерацій, складу морф життєвого циклу, а також шкодочинність *P. orientalis*.

Ключові слова: *Pineus orientalis*, інтродукція рослин, біологічні інвазії, повний цикл розвитку, побічний цикл розвитку, діпауза, циклічні морфи