

Features of bird-cherry that inhibits the breeding of the population *Rhopalosiphum padi* (L.) (Hemiptera: Sternorrhyncha: Aphididae)

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Abstract. Long-term studies (2012–2018) of the formation of the *Rhopalosiphum padi* (L.) heteroecious population (number of remigrants, oviparae and eggs in autumn, number of perished eggs, fundatrices larvae, timing of flight of emigrants in spring) on the two samples of primary host *Padus avium* Mill. and *P. avium* x *P. virginiana* (L.) characterized by various morpho-physiological features have been carried out. By the methods of mathematical statistics, it has been proved that this formation occurs under the significant influence of the year conditions (A), host plant characteristics (B) and these factors interaction (AB). The most visible was their highly significant impact on the number of wintering aphid eggs (A = 200.42; B = 142.6; AB = 25.612). Plant characteristics such as significantly larger leaf area from the middle part of the shoot on *P. avium* x *P. virginiana*, than on *P. avium* ($t = 8.37$; $p_{0.01} = 2.85$) was important for attracting remigrants and the prone buds on *P. avium* x *P. virginiana* - for oviposition and survival of eggs. Correlation between the period of leaf fall and number of aphid eggs on both bird-cherry samples is presented. The effect of weather conditions on *R. padi* and primary hosts relationships is discussed. Correlation ($r = 0.76$; $p = 0.0048$) between average temperature of October and eggs number on *P. avium* is given. *R. fundatrices*.

Key words: gynoparae, oviparae, eggs, fundatrices, emigrants, buds, host-plant, defoliation, year conditions.

INTRODUCTION

Showy flowering, ecological plasticity (widespread, frost resistance, resistance to environmental pollution, drought resistance), medicinal and nutritional value of *Padus* Mill. species attracts the attention of crop producers and breeders (Bezmenova et al., 2010; Simagin & Lokteva, 2012; Kishchenko, 2017). *P. avium* Mill and *P. virginiana* L. are easily interbred and are most widely used for breeding in Russia (Simagin & Lokteva, 2015). *P. maackii* (Ruor.), *P. ssiory* (Fr., Schmidt) C. K. Scneid, *P. serotina* (EhR.) Agardh. are also used in landscaping. In the European part of Russia, *Rhopalosiphum padi* (L.) belongs to the most economically important species of cereal aphids. As heteroecious (host-alternating) species, *R. padi* not only reduces the quantity and quality of grain crops harvest - summer hosts of aphids, but also affects ornamentality and

fruiting of bird-cherry, which is its winter host. In Europe, *R. padi* predominantly inhabits *P. avium*., in North America - *P. virginiana* and *P. pensylvanica* Loisel (Finlay & Luck, 2011). Aphids winter in the egg phase. In spring the fundatrices come out of the eggs, their numerous offspring causes twisting and yellowing of bird-cherry leaves, which persists until the defoliation even after complete aphids emigration to grasses. Despite the large number of works devoted to *R. padi*, the bird-cherry resistance to this pest remains unclarified. Current global climate changes increase the study relevance of trophic phytophages bonds including aphids with high ecological plasticity (Harrington et al., 2007).

The purpose of the study is the search for the bird-cherry characteristics limiting the number of *R. padi*.

MATERIALS AND METHODS

Perennial study (2011–2019) of the settlement terms and the generations number of *R. padi* in autumn (remigrants – gynoparae and males and sexual females - oviparae), as well as development of eggs and fundatrices in spring on agrestic specimen *P. avium* (7 trees) and *P. avium* x *P. virginiana* (5 trees) in conditions of similar pest flight background not far from each other (St. Petersburg-Pushkin; 59°43'N. 30°25'E) was carried out. The bird-cherry specimens differed from one another by morphological and vegetation periods. The trees (not less 25 years old) were the same every year. Eggs and aphid count in spring was carried out on not less than 100 annual shoots from various crown parts on each of the trees. The shoots were randomly selected and marked. The first counts were made before fundatrices hatching on the buds and later on the leaves after the start of their reproduction. The quantity of remigrants and oviparae was monitored in autumn on the leaves of at least 100 annual shoots randomly selected on the same trees. The accounting results were recalculated by 100 record buds or leaves to standardize data. Observations were carried out once a week until the end of leaf fall. Bird-cherry phenophases passage dates were noted, which are associated with periods of seasonal aphids' migration, egg laying and wintering generation release were noted. The lamina area and leaf buds' length from the middle part of the shoot were determined 20 times on each tree. The timing of aphids' emigration on grasses was determined on 15 trees of *P. avium* and *P. avium* x *P. virginiana* growing in Saint-Petersburg and in Leningrad oblast (2012–2018). In autumn 2019 due to technical reasons the accounting was made only for *P. avium* (all trees *P. avium* x *P. virginiana* were chopped down).

Information characterizing the course of environmental conditions during the research period are taken from web-sites <http://weatherarchive.ru> (temperature) and <http://www.pogodaiklimat.ru> (precipitation=rainfall). Some meteorological parameters that are particularly important for data analysis are given in Table 1.

The experiments results were processed with ANOVA using Statistica. *R.* The data obtained was described statistically by making a two-factor analyses of variance. The influence of temperature on *R. padi* eggs laying was assessed by Polynomial regression. The F (Fisher's) test was applied. Significance of differences between the mean values was determined using student's t-test.

Table 1. Selected meteorological data characterizing the years of research

Year	Month	Air temperature, °C						Rainfall, mm				Total
		Decade			Max.	Min.	Average	Decade			Max	
		I	II	III	(date)	(date)	of month	I	II	III	(date)	
2014	April	-0.3	5.7	8.7	20.0 (21)	-6.0 (2)	4.7	3.9	4.8	1.0	3.0 (6; 14)	9.7
	May	6.4	13.4	16.5	25.8 (20)	-1.0 (3)	12.1	14.0	13.7	64.7	32.0 (28)	92.4
	June	17.7	12.3	12.0	30.0 (6)	4.0 (18)	14.0	21.4	25.6	24.1	20.0 (30)	71.1
2016	April	4.9	5.3	7.4	18.0 (28)	-4.0 (4)	5.9	8.0	26.3	34.6	12.0 (29)	68.9
	May	13.9	11.1	14.6	18.3 (6)	3.0 (12)	13.2	0.0	2.3	28.0	15.0 (27)	30.3
	June	12.5	14.7	18.5	27.0 (26)	4.0 (7)	15.2	11.8	57.4	21.9	28.0 (16)	91.1
2017	April	4.6	-0.2	4.4	15.0 (10)	-9.0 (19)	2.9	13.8	18.1	55.2	15.0 (23)	87.1
	May	5.6	9.8	12.6	24.0 (19)	-2.0 (10)	9.3	1.0	1.1	11.3	7.0 (31)	13.4
	June	11.4	15.2	14.1	24.4 (17)	3.4 (2)	13.6	17.6	26.3	24.6	13.0 (21)	68.5
2011	September	14.6	13.1	11.7	21.2 (6)	6.2 (26)	13.1	28.4	45.0	43	26.2 (20)	116.4
	October	10.0	6.1	6.8	15.2 (1;7)	-0.8 (15)	7.6	17.4	26.6	1.0	14.1 (12)	15.0
	November	5.8						0.9			0.9 (7)	
2013	September	14.7	13.8	7.8	22.1 (1)	2.0 (30)	12.1	8.0	0.0	47.2	20.0 (23)	55.2
	October	9.0	5.7	7.1	13.9	-1.5(22)	7.3	7.6	8.0	53.4	9.0 (27)	69.0
	November	6.7			(5; 9; 10)							
2017	September	13.1	13.1	11.2	22.3 (12)	6.2 (28)	12.5	12.1	54.1	0.6	21.0 (13)	66.8
	October	8.6	7.2	1.4	11.7	-2.0 (23)	5.7	44.5	35.8	12.4	20.0 (9)	92.7
	November	2.8			(10;16;17)			3.0			2.0 (7)	
2018	September	18.0	14.9	10.6	27.0 (7)	1.1 (29)	14.5	10.6	38.6	19.8	14.0 (26)	69.0
	October	8.0	10.9	3.4	19.1 (15)	-3.0 (30)	7.4	16.1	0.2	10.5	5.0 (5)	26.8
	November	6.0						0.4				

RESULTS

The characteristics of bird-cherry samples included the duration of vegetation phases, location of buds on the shoot, bud length and leaf area from the middle of the branch and the presence of underbrush (Table 2–3).

Table 2. Characteristics of the bird-cherry samples

Sample	Vegetation times	Location of buds on the shoot	Bud length,	Leaf area	Presence of underbush
			mm*	(cm ²)**	
<i>Padus avium</i> x <i>P. virginiana</i>	late ripening (4–14 days later)	prone	10.1 ± 0.04 (a)	155.7 ± 7.3 (c)	lack
<i>P. avium</i>	mid ripening	erect	9.2 ± 0.1 (b)	114.9 ± 5.5 (d)	presence

Note: *– significant difference: $t = 4.47$; $p_{0.01} = 2.85$ (a–b); **– significant difference: $t = 8.37$; $p_{0.01} = 2.85$ (c–d).

We showed that in autumn gynoparae were the first to appear on both bird-cherry specimens, which further produce oviparae larvae. The earliest appearance of gynoparae was noted in the last decade of August, the latest - in early September. Usually males arrive 1–2 weeks later (Table 3) when the first oviparae mature.

Table 3. *Rhopalosiphum padi* (L.) development conjugation with primary hosts (2011–2018)

<i>R. padi</i>	Date *	<i>p. Padus</i>	Date	
Indicator		Indicator	<i>P. avium</i>	<i>P. avium</i> x <i>P. virginiana</i>
Fundatrices coming out of eggs	(30.03–15.04) - (14.04–21.04)	The beginning of the bud scale separation - appearance of green cones - budding	28.03–18.04	4.04–25.04
The beginning of the founder's reproductions	18.04–18.05	White buds - beginning of flowering	5.05–10.05	9.05–15.05
Timeline of emigration	(15.05–10.06) - (6.06–28.06)	Completion of flowering	10.05–1.06	17.05–20.06
Gynoparae remigration start	21.08–8.09	Timeline of the defoliation	(9.09–24.09) - (10.10–29.10)	(14.09–12.10) - (16.10–6.11)
The beginning of males' remigration	4.09–18.09			
Egg appearance	15.09–6.11			

* Note: brackets – phenoamplitude of the beginning and the end of the period represented in Indicator during years study.

The peak of remigrants (gynoparae and males) flight is usually observed in the second half of September-early October. The eggs appeared from the beginning to the end of defoliation, sometimes several days longer while the oviparae were alive. The formation of all the identified indicators was highly significantly influenced by the characteristics of the host plant, the years of research (excluding the mortality of the fundatrices larvae I–II age), as well as the interaction of both factors (Tables 4, 5).

Table 4. Two-factor analysis (Fisher's test) of number of remigrants, oviparae, eggs and dead fundatrices larvae I–II age in the years (A) and features of the bird-cherry samples (B)

Factor	Remigrants/100 leaves means ± SD	Oviparae/100 leaves means ± SD	Eggs/100 buds means ± SD	Dead fundatrices larvae I–II age, % means ± SD	
Factor A (years)					
1	74.8 ± 12.6	176.3 ± 43.9	281.5 ± 34.3	28.6 ± 2.3	
2	128.1 ± 19.3	383.6 ± 51.8	65.7 ± 6.3	41.5 ± 4.1	
3	29.2 ± 4.9	45.1 ± 4.6	87.4 ± 12.9	39.4 ± 4.5	
4	47.4 ± 5.6	185.9 ± 17.9	54.0 ± 4.7	40.2 ± 4.2	
5	60.5 ± 6.4	179.0 ± 11.3	64.2 ± 7.7	77.9 ± 3.9	
6	70.5 ± 12.9	228.3 ± 16.4	47.2 ± 6.1	24.2 ± 2.3	
7	8.3 ± 1.1	32.1 ± 39.0	28.5 ± 5.7		
8			10.9 ± 1.7		
Factor B (bird-cherry samples)					
1	81.2 ± 9.6	223.9 ± 27.1	105.2 ± 17.4	41.4 ± 4.1	
2	38.5 ± 3.9	127.6 ± 15.4	54.6 ± 8.6	42.5 ± 3.5	
Interaction AB					
1	1	110.4 ± 8.6	300.2 ± 30.8	379.8 ± 16.7	24.6 ± 2.3
1	2	39.2 ± 3.7	52.4 ± 6.1	183.2 ± 13.2	32.7 ± 3.3
2	1	184.0 ± 8.7	514.0 ± 56.1	80.8 ± 5.5	36.3 ± 5.8
2	2	72.2 ± 6.7	253.2 ± 20.1	50.6 ± 5.8	46.7 ± 5.2

Table 4 (continued)

3	1	38.2 ± 5.8	54.0 ± 5.0	114.8 ± 14.2	49.1 ± 5.4
3	2	20.2 ± 6.1	36.2 ± 5.5	60.0 ± 13.3	29.5 ± 3.9
4	1	59.2 ± 7.6	232.0 ± 15.3	64.6 ± 5.6	34.6 ± 5.9
4	2	35.6 ± 4.1	139.8 ± 12.4	43.4 ± 3.7	45.7 ± 5.4
5	1	61.2 ± 10.3	184.0 ± 15.1	81.7 ± 6.3	80.8 ± 5.4
5	2	59.8 ± 8.9	174.0 ± 18.4	46.7 ± 8.7	75.0 ± 5.7
6	1	105.0 ± 12.0	242.0 ± 25.1	64.5 ± 3.3	23.1 ± 3.3
6	2	36.0 ± 4.1	214.6 ± 21.9	30.04 ± 2.8	25.1 ± 3.4
7	1	10.2 ± 1.7	41.2 ± 4.4	41.1 ± 7.4	
7	2	6.4 ± 0.9	23.0 ± 2.8	15.8 ± 3.2	
8	1			14.2 ± 2.2	
8	2			7.7 ± 1.5	

Note: A (1 – 2012, 2 – 2013, 3 – 2014, 4 – 2015, 5 – 2016, 6 – 2017, 7 – 2018, 8 – 2019 years); B (1 – *Padus avium* x *P. virginiana*, 2 – *P. avium*).

Table 5. Results of two-factor analysis (Fisher's test) of number of remigrants, oviparae, eggs and dead fundatrices larvae I–II age in the years (A) and features of the bird-cherry samples (B)

Factor	Remigrants/100 leaves		Oviparae/100 leaves		Eggs/100 buds		Dead fundatrices larvae I–II age	
	F	p	F	p	F	p	F	p
A	58.149	0	58.505	0	200.42	0	32.072	0
B	127.18	0	68.016	0	142.46	0	0.1505	0.69977
AB	17.405	0	13.003	0	25.612	0	3.1948	0.01436

At the same time, the influence of the host plant on the remigrants and oviparae number during its peak was higher than the dependence on the year. It was noted that the number of *R. padi* eggs were most influenced by both factors and their interaction. The influence of the bird-cherry sample on the remigrants number (Table 4–5) may be caused by leaf area. The larger leaves of the hybrid (Table 2) attracted aphids more strongly than the leaves of *P. avium*. It was shown that the number of eggs was determined by the timing of the leaf fall end. Late leaf fall was more favorable for oviparae oviposition on both bird-cherry samples (Fig. 1–2). On *P. avium* x *P. virginiana* buds, oviparae have always laid more eggs than on *P. avium*.

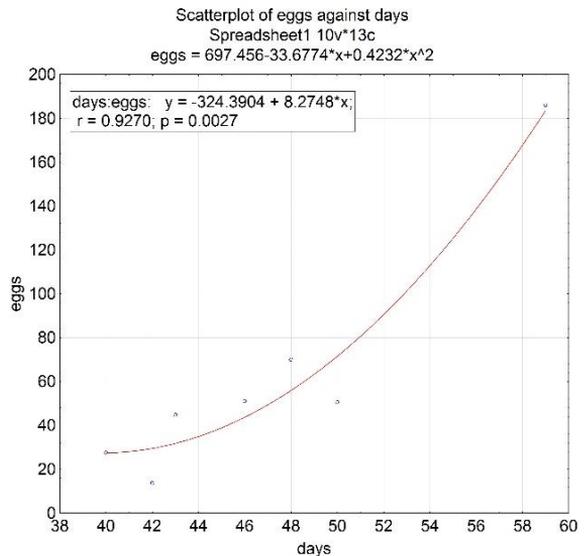


Figure 1. Correlation between the duration of leaf fall on *P. avium* and *R. padi* laid eggs.

In general, later leaf fall on *P. avium* x *P. virginiana* (16.10–6.11) than on *P. avium* (10–25.10) was leading to larger eggs on first sample (Table 4–5). In particular, autumn 2011 was characterized by a very late leaf fall (up to 6.11), which resulted in the maximum of eggs in spring 2012. Egg numbers declined in subsequent years. We determined the dependence between the average daily temperatures for October and the number of eggs (Fig. 3).

In 2012–2017, the number of laid eggs was significantly higher near each populated prone and longer *P. avium* x *P. virginiana* buds (Table 2), than near erected and shorter *P. avium* ones (4.3 ± 0.91 and 2.05 ± 0.44 eggs/populated bud, respectively: $t = 2.47$; $p_{0.05} = 2.45$). After 2012, the number of aphid eggs decreased and was the lowest in 2017–2018 (Table 4). Possible reasons could include a lot of spiders (up to 20 individuals/100 shoots in autumn 2013–2014), as well as urbanization. Over the research years in spring, eggs generally died to a greater extent near buds erect from shoots than those prone (14.5 ± 1.4 and 7.8 ± 1.2 respectively $t = 3.72$; $p_{0.01} = 3.50$).

However, in 2017, when the amount of April precipitation was 87.1 mm - 278% of the norm (Reference and information portal ‘Weather and Climate’), the number of dead eggs along prone buds was higher (7.9 ± 0.3 and 0.61 ± 0.13 respectively $t = 12.42$; $p_{0.001} = 5.96$) due to their soaking. The fundatrices fundatrices hatch from eggs and their future fate were largely determined by the conjugation of insect development with the host plant phenology (Table 3). Vegetation of *P. avium* is known to begin at temperatures above 0 °C, and *P. virginiana* - at +5.2 °C (Kishchenko, 2017). In hybrids, the threshold temperature can vary, but is always higher than

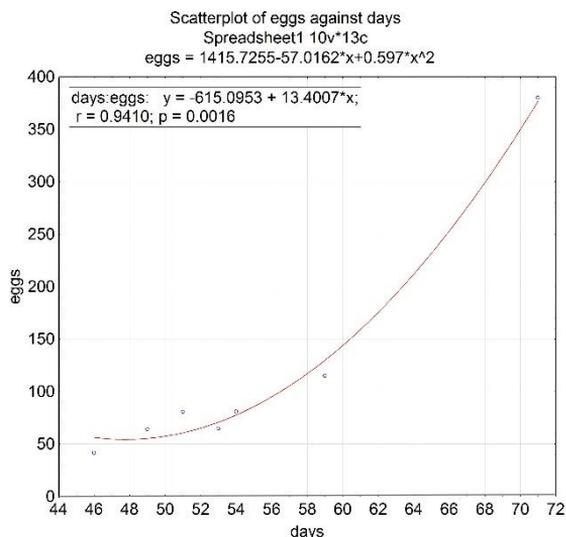


Figure 2. Correlation between the duration of leaf fall on *P. avium* x *P. virginiana* and *R. padi* laid eggs.

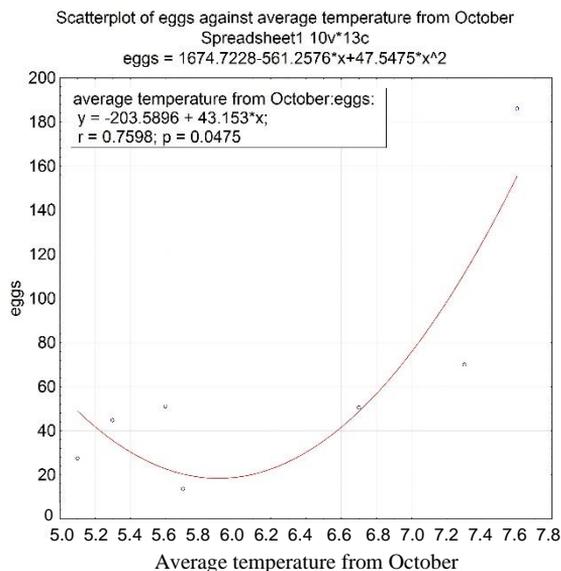


Figure 3. Correlation between the average temperature from October and *R. padi* eggs number on *P. avium*.

that of *P. avium*. The threshold temperature for the development of *R. padi* is considered +4.5° (Bokina, 2009). The first fundatrices fundatrices' larvae may massively die if they hatch from eggs before the appearance of green cones and budding on *P. avium* x *P. virginiana*, as happened in 2014. (Fig. 4).

High mortality of younger fundatrices larvae on *P. avium* x *P. virginiana* in 2017–2018 was associated with low temperatures, excessive precipitation in April and delayed budding, which is essential not only for feeding, but also for the fundatrices larvae shelter. In 2015–2016, fundatrices larvae on *P. avium* survived to a lesser extent. fundatrices.

The ambiguous influence of the bird-cherry sample on the death of fundatrices larvae in different years became the reason for its statistical insignificance (Table 5).

The fundatrices reproduction beginning and the increase in the colonies' population coincides with the phase of 'white buds' and the beginning of bird-cherry flowering. The duration and intensity of emigration is largely determined by the timing of the host's flowering (Table 3). As a rule, the emigrants flight began in the second half of May and ended in the first decade of June. The deadline for the end of emigration was marked in 2017 and was associated with weather conditions (see above). The duration of emigrants' flight in different years was 17–39 days. With the end of flowering, aphids leave bird-cherry, although they can reproduce through the season on the underbrush.

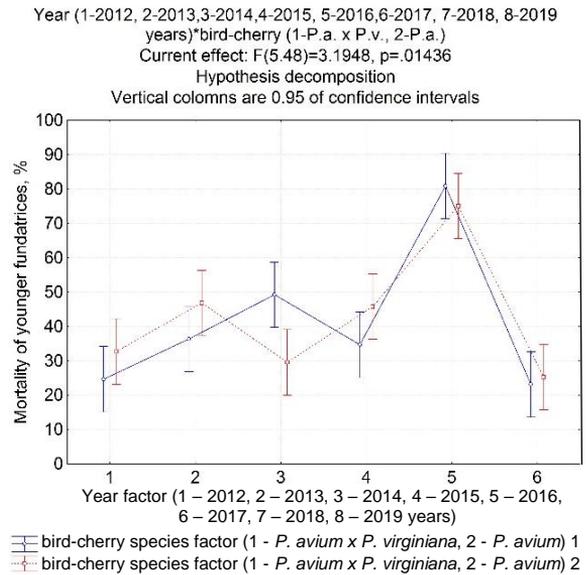


Figure 4. Number (%) of dead fundatrices larvae I–II age *Rhopalosiphum padi* (L.).

DISCUSSION

Heterecia (seasonal change of host) in aphids life cycles developed in the process of long-term joint phylogenesis with plants. In the typical case, trees or shrubs were more ancient (primary), secondary - grasses (Shaposhnikov, 1987; Williams & Dixon, 2007) - very systematically distant from each other plants. According to the modern classification, they are often included not only in different orders, but also classes (APG III, 2009). Heterecia includes spring aphids' emigration to grasses and autumn remigration to the primary host - the only one on which the first overwintered generation (fundatrices) can survive. It can be assumed that the ability of woody plants to survive from year to year in mass aphids breeding conditions is the result of prolonged strict selection accompanied by their self-protection formation (Aphids on the world's plants. An online identification and information guide). The basis for selection was trophic relationships of hosts and phytophages. Aphids are characterized by feeding in areas of

inflow or outflow of assimilates, i.e. on growing or aging plants (Dixon, 1998). Thus, the very emergence of heterocia is associated with the onset of a period unfavorable for aphids feeding, when active seasonal growth of the woody host ends. On the contrary, aphids' autumn remigration coincides with the period of leaf life end. To have time to lay their eggs, aphids begin to leave the grasses long before the defoliation start. The limited range of primary hosts, their large size, distance from grasses, clonal differences in the timing of remigrations in aphids contribute to sexes meeting and prevent inbreeding. Often, remigrants guided by the smell of plant leaves. It was no coincidence that the large leaves of *P. avium* x *P. virginiana* were more attractive to gynoparae than the smaller ones - *P. avium*. Males appeared later. It is assumed that they are also guided by oviparae pheromones and volatile substances associated with aphid aggregation (Pickett & Glinwood, 2007). Other authors note variants where *R. padi* males appear earlier than gynoparae and may be attracted only by the plant (Austin et al., 1996). However, early appearance of males is not biologically justified, as the preimaginal period in oviparae is 7–11 days, and life expectancy from 19 to 47 days is enough for the sexes to meet (Vereschagina & Gandrabur, 2016). Oviparae have been shown to be able to anticipate defoliation and migrate in time (Glinwood et al., 2003), but they cannot control windy weather and massively fall with leaves, especially on *P. avium* with early growing terms.

Long prone buds on hybrid shoots are also more favorable for laying eggs as eggs are laid along the buds. The overall decline in egg numbers over the years of research may have occurred not only due to rapid defoliation due to cold and windy weather, but also the abundance of entomophages, especially spiders, elimination of habitats of aphids agrestic hosts as a result of large-scale construction, increase of the power lines length, placement of cell towers, as well as other external and intra-population factors.

In the spring, the fundatrices hatch from eggs before budding leads to high larvae mortality of younger larvae as we observed on the late ripe *P. avium* x *P. virginiana*. Hence, it is necessary to clarify the forecast of the pest population based on the number of eggs without considering the death of the overwintered generation. The fundatrices begin reproduction with the appearance of white buds on bird-cherry, by mass flowering the colonies population rapidly increases, the first emigrants appear. Simultaneously with the end of flowering, bird-cherry ends active growth of leaves and inflorescences (Kishchenko, 2017), the decrease in the flow of assimilates to available feeding places combined with the high number of aphids cause them to complete emigration. It is possible that the damaged bird-cherry may release substances that contribute to aphids' emigration (Pickett & Glinwood, 2007), but insects did not move to intact leaves or between trees during the flowering phase. Late and prolonged bird-cherry flowering increases the duration of the aphids' flight, as at this time aphids feed mainly on inflorescences as we observed on both bird-cherry specimens. Due to different reactivity of plants and insects on global climatic changes there are significant disturbances in the conjugation of their phenologies. The likely adverse effects of such disturbances can be reduced by revising the pest monitoring methods and the use of resistant plants.

CONCLUSION

Based on long-term comparative study on the development of *R. padi* on *P. avium* and *P. avium* x *P. virginiana*, characterized by different morpho-physiological features

(statistically established), it was shown that later vegetation onset, rapid passage of vulnerable development phases (before flowering end), early leaf fall, as well as lack of underbrush, buds erection from the shoot, small laminas deter reproduction of aphids on the bird-cherry.

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