ACTA Acta Sci. Pol. Hortorum Cultus, 16(1) 2017, 39–49
www.acta.media.pl ISSN 1644-0692

ORIGINAL PAPER
Accepted: 3.08.2016

MORPHOLOGY, BIOLOGY AND BEHAVIORAL ASPECTS OF *Aphis craccivora* (HEMIPTERA: APHIDIDAE) ON *Robinia pseudoacacia*

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ABSTRACT

The bionomy and ecology of *Aphis craccivora* on *Robinia pseudoacacia* was studied. The number of generations per year was determined, as well the lifespan of a generation and fecundity of the females. For the first time the strategy of development of a dangerous pest has been determined which enables it to spread worldwide. *A. craccivora* is a cosmopolitan species. It is a polyphagous insect settling on over fifty different plant species across nineteen families. It settles on green plants and trees of the Leguminosae family. It is considered to be one of the most important pests of crops causing great losses to yield. The cowpea aphid adapts to changing environmental conditions, particularly to high temperatures as well as to different host plants. Its adaptation strategies can be seen in its biology, morphology and behaviour. The main adjustment is the production of even up to 15 generations per year, high fecundity, ability to form dwarf morphs, and settling not only green plants but also trees. These features enable this species to expand and adjust to new conditions and new plants.

Key words: cowpea aphid, bionomy, *Robinia pseudoacacia,* strategy, adaptation, developmental stages

INTRODUCTION

Cowpea aphid, *Aphis craccivora* Koch, is considered to be one of the most common and best known plant pests around the world [Minks and Harrewijn 1987]. It occurrence is widespread but probably originated in warm, temperature areas of the Palearctic [Blackman and Eastop 2000]. *A. craccivora* is recorded on all continents, in Asia, the Americas, Europe and Africa [Berim 2009], as well as in Australia [Gutierrez at al. 1971]. It is one of the relatively few aphid species with pest status in the tropics [Jaba et al. 2010]. Cowpea aphid can develop anholocyclically, especially in warm temperate and tropical regions. In countries with a temperate climate, it is a holocyclic, not host-alternating species [Heie 1986]. Sexual generation comprises wingless oviparous females and alate males. *A. craccivora* is a polyphagous insect which prefers plants of the Leguminosae family. It was shown in fifty host plants of nineteen families [Mehrparvar et al. 2012]. It can settle on green plants of the following genera: *Lupinus*, *Medicago*, *Melilotus*, *Trifolium*, *Vicia*, and on certain trees: *Caragana* and *Robinia.* It has also been recorded on plants from other species, e.g. *Capsella bursa-pastoris* (L.) and *Rhamnus cathartica* L. [Heie 1986]. It is a serious pest in vegetable farming and one of the most serious pests for cowpea, *Vigna unguiculata* (L.),

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causing huge losses in yield [Kamphuis et al. 2012]. *A. craccivora* has also been reported to be a pest for peanut crops in Africa [Herselman et al. 2004, Berberet et al. 2009] and in Pakistan [Javed et al. 2014]. In Australia cowpea aphid has been reported to infest pasture vegetables, for example, *Trifolium subterraneum* L., *Medicago* sp., *Lupinus angustifolius* L. [Nair at al. 2003]. By sucking out the sap from leaves, flowers, shoots and pods, aphids directly reduce crop yields. Indirect harm is associated with the transmission of over fifty kinds of plant viruses [Stoetzel and Miller 2001]. The most important ones are: Groundnut rosette virus (GRV), Subterranean cloves stunt virus (SCSV), Bean common mosaic virus (BCMV), Cucumber mosaic virus (CMV). These viruses are the cause of economic damage to vegetables, for example, in California and Arizona [Natwick 1999], in Arkansas, in the United States [Capinera 2001], in Taiwan [Chen et al. 2013] and in Algeria [Laamari et al. 2008].

Among aphids, *A. craccivora* is one of the most frequently described and researched species. Many papers are concerned with the aphid's morphological aspects [Mehrparvar et al. 2012, Mier Durante et al. 2012], biological aspects [Obopile and Ositile 2010, Ryalls et al. 2013, Soffan and Aldawood 2014], the impact of temperature on their development [Berg 1984, Kuo and Chen 2004, Chen et al. 2009, 2013], or plants' resistance to this aphid species [Hafiz 2006, Laamari et al. 2008, Kamphuis et al. 2012, Aliyu and Ishiyaku 2013, Souleymane et al. 2013, Ryalls et al. 2013]. This undoubtedly confirms the fact that it is one of the most important and dangerous plant pests, being a cosmopolitan species easily adapting to different temperatures and hosts plants. In spite of much research on this species so far one has not been able to state why *A. craccivora* has a status of a dangerous pest and what is its strategy which enables it to expand.

The aim of this paper was to study the bionomy of *A. craccivora* on *Robinia pseudoacacia* and determine the number of generation per season and fecundity within particular generation. The next aim is to present the strategy of *A. craccivora* adaptation to the changing environmental conditions in temperate climate, taking into consideration the biological, morphological and behavioural aspects.

MATERIALS AND METHODS

The impact of temperature on the development

Research on the impact of temperature on the development of *A. craccivora* was performed in field conditions in Poznan, midwestern Poland over three consecutive growing seasons. Aphids were isolated on the shoots of *Robinia pseudoacacia* L. A single virginopara was placed under each isolator made from nylon gauze. The first instar nymph born initiated a new generation. The virginoparae of each generation were transferred, being placed under a new isolator, where their fecundity was tested. During the individual lifespan of the virginoparae from each generation, the length of their developmental cycle was studied (time of pre-reproduction, reproduction and post-reproduction). In each generation the growth of ten females was researched. The observations were carried out from April until the end of November. Meteorological data was obtained from the Poznan city district Weather Station, 3 km away from the site of the research.

The impact of temperature on morphology

The materials constituted the nymphal stages, alate and apterous viviparae. The subsequent stages of aphids were collected after moulting. *A. craccivora* was reared on the *R. pseudoacacia* in the spring and summer. Microscope samples were made from the collected material. Five morphological features were analyzed, for 10 specimens in each stage. The following parameters were measured: body length (BL), hind tibia length (TL), the length of the third segment of the antennae (Ant. Seg. III), antennae length (Total Ant.), and rostrum length (R).

Statistical analysis

For a comparison of length of particular life cycles and fecundity of subsequent aphid generations (G1-G14) a Kruskal-Wallis test was used. To show the dependency between aphids' fecundity and temperature (mean daily and maxiumum daily) a Pearson correlation was used. In order to show morphological differences between spring and summer morphs a U Mann-Whitney test was used.

The statistical analysis of the data was performed using StatSoft, Inc. [2010], STATISTICA, version 9.0, www.statsoft.com.

RESULTS

During the course of the research, on average 14 generations of virginoparae *Aphis craccivora* were recorded in growing season (fig. 1). Mean length of pre-reproduction period ranged from 8 days in the G8 generation to 19 days in generation G14 (fig. 1a). A negative correlation of the duration of the pre-reproduction period of *A. craccivora* was found with maximum temperature (R = -0.598; p = 0.00) and mean daily temperature (R = -0.576; p = 0.00). Generations developing in higher temperatures typically

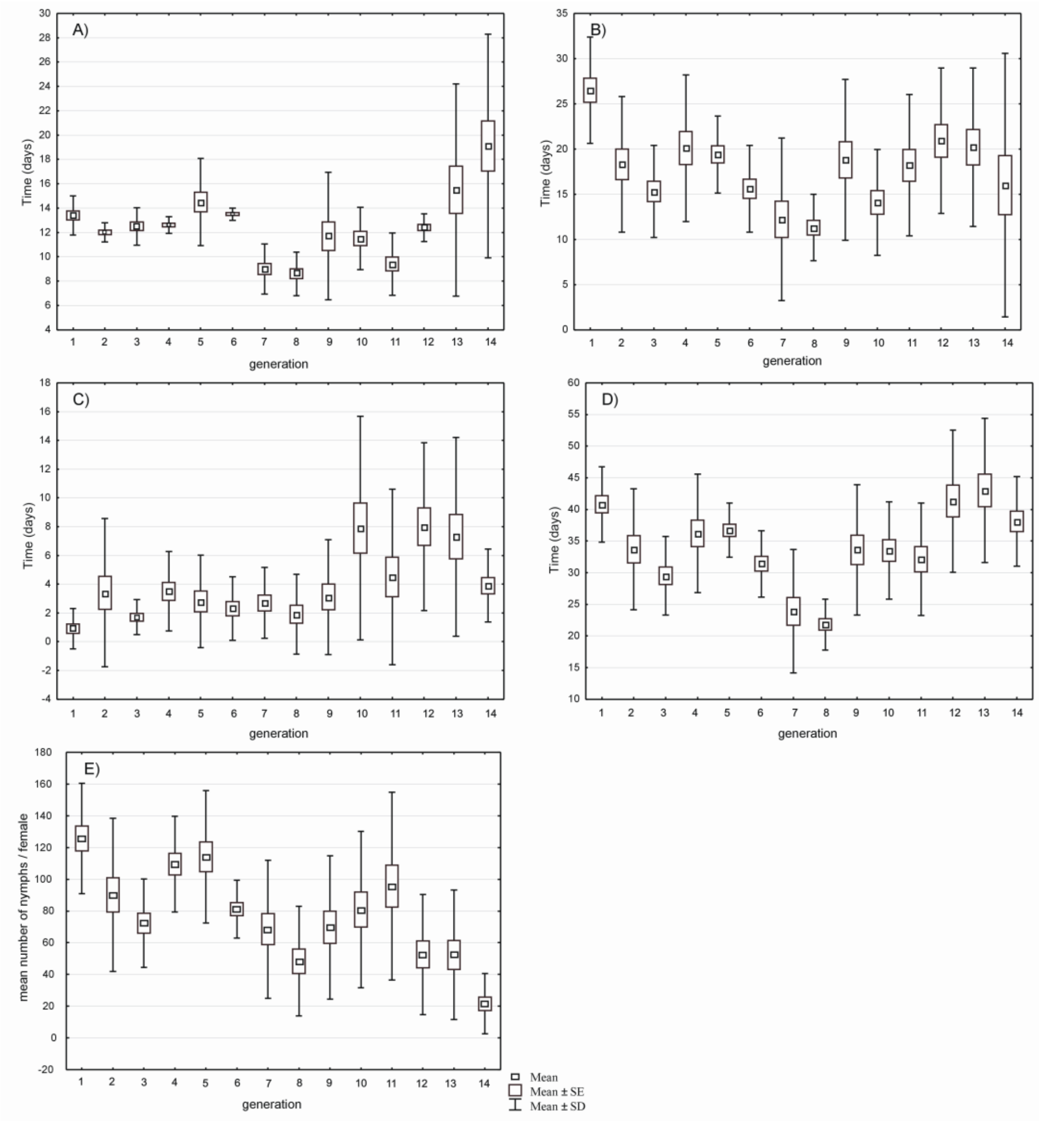

Fig. 1. The mean time of development of subsequent-generation *Aphis craccivora*: (A) prereproduction, (B) reproduction, (C) postreproduction, (D) longevity and (E) fecundity. G1–G14: generations

had a shorter pre-reproduction period, especially during the high temperature period in July.

The longest reproduction period was observed in the first generation G1 (fundatrices) and was on average 27 days. The shortest birth-giving time was registered during the summer when high temperatures were recorded, in the G8 generation, when the period was on average 11 days (fig. 1b). The post-reproduction period was rather short and took on average from 1 to 8 days (fig. 1c). Its lengthening was observed in autumn as temperatures decreased. The entire longevity of *A. craccivora* ranged on average from 21 days in the G8 generation to 43 days in the G13 generation (fig. 1d).

Most *A. craccivora* generations were typically highly fertile (fig. 1e). The highest fecundity was observed among fundatrices (G1) which on average gave birth to 125 nymphs. The lowest fecundity was recorded among the G14 generation – on average 20 nymphs per female. A correlation of fecundity between *A. craccivora* and daily maximum and mean temperatures was observed (R = 0.37750; p = 0.0001). Together with an increase in temperature, female fecundity grows until optimum temperatures are reached at 18–20°C (fig. 2).

All the researched morphs which were observed during spring differed from the ones observed in the summer (fig. 3). High temperatures had a great impact on stunting of specimens whose morphological parameters were clearly smaller than in spring morphs (tab. 1). The greatest differences were shown to occur among the larvae of the I stage (fig. 4). Spring and summer larvae of the I stage differed statistically significantly in their body length (Z = -3.25; p = 0.001), tibia length (Z = -3.74; p = 0.0001), length of the III segment of antennae (Z = -3.74; p = 0.0001), entire length of antennae (Z = 3.74; p = 0.0001) and length of rostrum (Z = -3.25; p = 0.001). Larvae of the II and IV stages significantly differed among themselves in body length, for II and IV stages (Z = -2.23; p = 0.02), (Z = -2.23; p = 0.025) respectively. Winged specimens differed significantly in tibia length (Z = -3.59; p = 0.0001). No significant differences in morphological parameters of the nymphs of the III instar and wingless females developing in spring and summer were found.

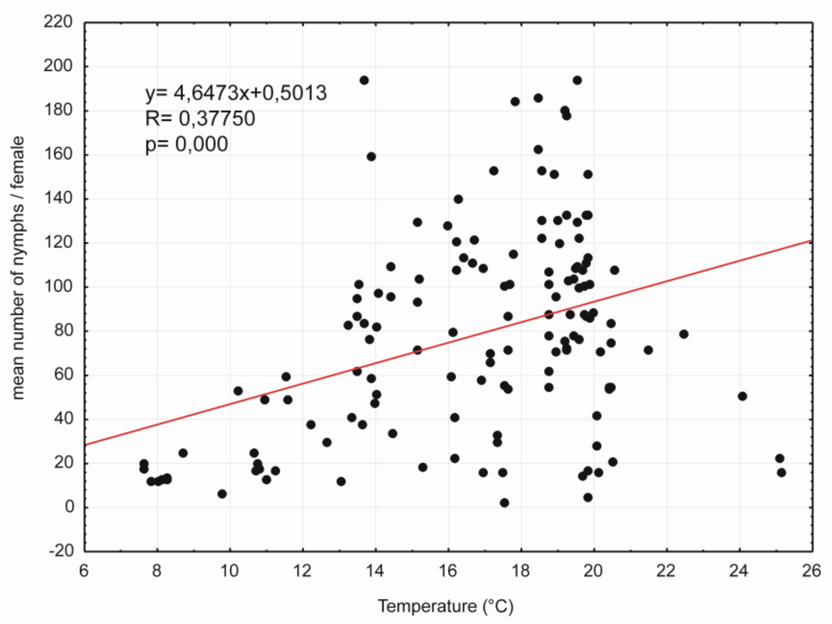

Fig. 2. Relation between the fecundity of *A. craccivora* on *R. pseudoacacia* and the daily mean temperature (°C)

Table 1. Morphological parameters of developmental stages *A. craccivora* (mm) in spring and summer

			Spring developmental stages		Summer developmental stages	
			range (mm)	mean (mm)	range (mm)	mean (mm)
Body length (BL)	1st	larval instar	0.64–0.82	0.72a	0.43–0.56	0.477b
	2nd		0.95–1.2	1.075a	0.77–0.9	0.836b
	3rd		1.35–1.6	1.431a	1.05–1.18	1.139a
	4th		1.4–1.9	1.707a	1.15–1.22	1.182b
	wingless females		2.0–2.4	2.2a	1.4–1.9	1.627a
	winged females		1.75–2.15	2.053a	1.22–1.5	1.374a
Hind tibia length (HT)	1st	larval instar	0.25–0.29	0.269a	0.12–0.2	0.18b
	2nd		0.32–0.41	0.369	0.32–0.39	0.36
	3rd		0.5–0.6	0.544	0.41–0.52	0.469
	4th		0.54–0.8	0.715	0.43–0.55	0.503
	wingless females		1.05–1.22	1.14	0.72–1.05	0.924
	winged females		0.92–1.22	1.073a	0.7–1.02	0.88b
Length of third antennal segment (ant. segm. III)	1st	larval instar	0.12–0.16	0.136a	0.09–0.11	0.096b
	2nd		0.12–0.2	0.148a	0.11–0.13	0.115a
	3rd		0.22–0.29	0.236a	0.16–0.23	0.205a
	4th		0.15–0.22	0.201a	0.12–0.19	0.147a
	wingless females		0.36–0.44	0.4a	0.22–0.4	0.297a
	winged females		0.29–0.37	0.339a	0.22–0.32	0.262a
Total lenght of antenna (total ant.)	1st	larval instar	0.34–0.4	0.365a	0.26–0.33	0.293b
	2nd		0.49–0.65	0.532a	0.45–0.52	0.482a
	3rd		0.69–0.79	0.722a	0.59–0.73	0.648a
	4th		0.75–1.12	0.959a	0.61–0.83	0.711a
	wingless females		1.22–1.45	1.355a	0.87–1.25	1.068a
	winged females		1.17–1.4	1.306a	0.87–1.25	1.105a
Rostrum length R	1st	larval instar	0.09–0.1	0.098a	0.07–0.08	0.078b
	2nd		0.1–0.11	0.104a	0.08–0.1	0.094a
	3rd		0.11–0.12	0.113a	0.09–0.11	0.1a
	4th		0.11–0.12	0.116a	0.09–0.11	0.098a
	wingless females		0.11–0.12	0.117a	0.1–0.12	0.107a
	winged females		0.1–0.12	0.108a	0.09–0.11	0.099a

Fig. 3. Spring female (A) and summer stunted female (B)

Fig. 4. Spring larvae (A) and summer stunted larvae (B) of I instar

DISCUSSION

The current approach to climate change suggests that due to doubled concentration of carbon dioxide, the mean temperature on Earth in the 21st century may increase by 1.7–5.3°C [IPCC 2007]. Aphids are some of the most sensitive of organisms to all environmental changes [Mackoś-Iwaszko et al. 2015]. They are plastic ecologically and may serve as bioindicators for changes taking place in the environment [Dixon 1998]. Temperature and humidity impacts insects directly by either stimulating or inhibiting the activity of imago or larvae, insect dispersion, phenology of appearance, development length or survival given unfavourable weather conditions. An indirect impact of climate change is concerned with the impact of climate on the insect environment, such as the quality of host plants, predator, parasitoid and pathogens activity [Jaworski and Hilszczański 2013]. During the course of their evolution, aphids have developed mechanisms allowing them to immediately react to the changing conditions of the environment. Climate warming influences faster population growth, the shortening of individual development, earlier hatching, lengthening of some generations development, longer development of parthenogenetic forms as well as changes in life cycles [Dixon 1998, Harrington et al. 2007, Strażyński and Ruszkowska 2015]. Adaptation strategies are evident in the morphology, biology and behaviour of these insects which our research confirms.

Stunting of aphids is one of the effects of high temperatures, which confirms the evolutionary trend to decrease the body of aphids in reaction to a predictable tendency of global warming [Dixon 1998, Chen et al. 2013]. Studying the biology of *Aphis craccivora* on *Robinia pseudoacacia*, four nymphal instars were observed. This is also confirmed by research by Behura et al. [1976] and Obopile and Ositile [2010]. Larvae, as well as wingless and winged females of *A. craccivora*, which were under observation, were much bigger than those observed in summer. Temperature can have considerable effects on morphological characters such as body size. *Aphis idaei* v.d. Goot on raspberry [Borowiak-Sobkowiak 2005] is another species which is stunted in the summer period. Insects at low latitudes are most likely to suffer decreases in growth, during the summer, when they are exposed to the highest, potentially lethal, temperatures, and to the longest periods of high, sub-lethal temperatures [Chen et al. 2013].

Climatic warming has the greatest impact on the development and the number of aphid generations in comparison with other insects [Harrington et al. 1995]. An increase in effective temperatures by 2°C increases the number of additional generations by 5 [Yamamura and Kiritari 1998]. *Aphis craccivora* on *R. pseudoacacia* forms on average 14 generations developing parthenogenetically from the end of April until October. The number of generations is much higher in comparison with another species on *R. pseudoacacia*. *Appendiseta robiniae* (Gillette) during one season forms on average 9 generations [Borowiak-Sobkowiak and Durak 2012].

Genetic change in this species has resulted in the failure to produce sexual forms [Ofuya 1997]. Gilbert and Gutierrez [1973] provide theoretical consideration to the function of sexual reproduction in stabilizing ecological relationship, by tending to maintain biological parameters at or near optimal values for survival. In Poland, in moderate climates, *A. craccivora* produces a sexual generation during autumn which enables it to survive unfavourable, low temperatures by inclusion of an egg stage. Cowpea aphid typically has a fast rate of development and a high reproductive potential in comparison with other species. The developmental time from birth to reproduction on alfalfa is on average 5.9 days at a temperature of 24°C [Berberet et al. 2009], whereas on *Vicia fabae* L., at a temperature of 20°C, it lasts from 7 to 10 days [Traicevski and Ward 1994]. Similar results were observed for *A. craccivora* on *R. pseudoacacia*. The shortest pre-reproduction time, which was 7 days, was registered for viviparous females developing in the summer.

The greatest fecundity (on average 125 nymphs/female) was found in the first generation of fundatrices. A similar tendency was also observed in other aphid species developing in the moderate climate of Poland, including *Amphorophora idaei* Börner [Borowiak-Sobkowiak 2006], *Cinara* (*Cupressobium*) *cupressi* (Buckton) and *C.* (*C.*) *juniperi* (De Geer) [Durak et al. 2007, 2015], *Brachycaudus divaricatae* Shaposhnikov [Wilkaniec and Wilkaniec 2013]. High fecundity was also common in spring generations. In Taiwan, at 25°C, fecundity of *A. craccivora* was lower and amounted to 97 offspring per female [Kuo and Chen 2004], in Africa on *Vigna unguiculata*, female fecundity may reach 100 or more progeny [Ofuya 1997]. High temperatures also impact the shortening of pre-reproduction and reproduction periods which leads to a lowering of fecundity.

One can suppose that the lowering of *A. craccivora* fecundity during hot weather in Poland is a strategy of this species, enabling its survival as the energy is used for surviving rather than reproduction.

Moreover, as a result of global warming, it is possible that large numbers of aphid nymphs survive to adulthood, but most adults could fail to reproduce resulting in a smaller population during the summer months [Chen et al. 2013]. These authors predicted that *A. craccivora* longevity and reproduction would decrease as the summer temperatures increased.

For the cowpea aphid, the optimal temperature range for reproduction on alfalfa is 18–24°C [Berberet et al. 2009], while on *Vicia faba* 25°C [Berg 1984]. Our research results correspond with the above. *A. craccivora* on *Robinia pseudoacacia* shows the greatest fecundity at temperatures ranging between 18–20°C. The development of *A. craccivora* is limited from temperatures of 35°C [Chen et al. 2009]. In moderate climate zones, temperatures above 30°C limit development and produce a significant drop in numbers. However, temperatures above 35°C cause high mortality in a short period of time. *A. craccivora* is capable of surviving in such hot temperatures, which is confirmed by results of research carried out on *Vigna sesquipedalis* (L.) by Kuo and Chen [2004]. Yet aphids lived for a very short time and gave birth to very few larvae at such temperatures.

A. craccivora is a polyphagous insect settling on green plants and trees. It is a widespread species, observed across the world, showing a broad range of adaptability to the host plant. It is one of the most important field pests of cowpea in Africa, Asia and Latin America, causing large economic losses in harvest [Ofuya 1997]. Several dozen or so years ago cowpea aphid was not considered to be an important pest of legumes in the United States. However, the status of this species as a pest for alfalfa has changed within the last 10 years. Recently its population grew significantly [Berberet et al. 2009]. Also, during the last decade, in West Africa, the population of *A. craccivora* has been increasing continuously [Ofuya 1997].

Due to their rapid developmental rate, high reproductive potential and their ability to transfer viruses, many researchers studied the growth of this species on crops. However, to our knowledge there has been no paper studying the biology and ecology of *A. craccivora* on *Robinia pseudoacacia*. It is a very expansive species from North America, and is treated in Poland as an invasive one. The plant has few demands, is resistant to drought, salty soil and environmental pollution. In Poland this tree is grown in gardens and urban greeneries because of its fast growth rate. It is also popular in forests. It forms a dense root system and so is used to forest degraded areas.

In the course of the research we observed the formation of large aphid colonies on *Robinia pseudoacacia*. What followed was the appearance of winged forms which colonized neighbouring plants. Gutierrez et al. [1974] suggested that *A. craccivora* has an exceptionally high potential for migration. The alate females are take the primary responsibility for finding a new host, but behaviour of this species shows their non-preference to already infested leaves [Jaba et al. 2010]. This strategy enables the cowpea aphid to settle and colonize other plants and expand the range of their host plants.

The morphological character of aphids is very important in adaptation to various host plants. Mehrparvar et al. [2012] found morphometric differences between populations of *A. craccivora* in Iran on different host plants. The authors suggest that the aphids population associated with *R. pseudoacacia* was cleary separated from other populations. The authors concluded that *A. craccivora* populations are not homogenous morphological entities and represent different host-associated forms.

Mehrparvar et al. [2012] showed that the length of siphunculus in *A. craccivora* associated with *R. pseudoacacia* is considerably larger in comparison with specimens developing on other plants. The authors suggest that the length of siphunculi might be in accordance with population adaptation to environmental conditions. The siphunculus releases alarm pheromone, so it is probable that aphids with longer siphunculi are able to release the alarm pheromone over a wider space [Mehrparvar et al. 2012]. Another adaptation element of *A. craccivora* to trees is a longer rostrum. The length of rostrum in aphids must be longer in order to penetrate deeply into the plant tissue [Mehrparvar et al. 2012].

Changes in climate can contribute to adaptation, growth in population number and expansion of species which are better adapted to new conditions.

A. craccivora, as one of the few aphid species of tropical status, shows a range of adaptation strategies. They concern morphology, biology and behaviour. It is a species which can survive in very high temperatures. It reacts quickly to climatic changes by means of a short growth cycle and high fecundity. Along with climate warming it may thus become an invasive species expanding range of host plants.

CONCLUSIONS

1. *A. craccivora* characteristically has a fast rate of development and high reproduction potential. Produces even up to 15 generation per year.

2. The optimal temperature range for their development is between 18–20°C.

3. *Aphis craccivora* adapts to changing environmental conditions, particularly to high temperatures (ability to form dwarf morphs) as well to different host plants.

4. Adaptation strategies of *Aphis craccivora* can be seen in its morphology, biology and behaviour.

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