INTRODUCTION

Insects are ectothermal entities whose activity is dependent on the temperature of the environment in which they exist (Bale et al., 2002). Aphids, which are ecologically flexible organisms, show a fast reaction to environmental changes (Dixon, 1998; Hulle et al., 2010). Abiotic factors which significantly impact their development include temperature, photoperiod, and humidity. Warmer temperatures, which significantly impact their development, include temperatures of 10, 15, 20, and 25°C, 75% humidity and photoperiod 16L:8D. The higher the temperature, the shorter the observed length of the pre-reproductive period, ranging from 6 days at 28°C up to 24 days at 10°C. The reproductive period also became shorter with the increase in temperature. A. craccivora female fecundity was dependent on temperature. The highest recorded rate of fecundity was observed when the temperature was 20°C (on average 115 larvae/female). The developmental threshold was calculated to be 3.3°C. The intrinsic rate (\(r_m\)) was maximal (0.42) at 28°C and minimal (0.07) at 10°C. With increasing temperature there is a finite rate of increase, and the mean rate of generation development shortens. The research suggests that the best range of temperatures for the development of A. craccivora on R. pseudoacacia is between 20-28°C. Therefore, in the future, with climate warming, A. craccivora may become more problematic.

KEY WORDS: cowpea aphid, life table parameters, fecundity, biology, black locust

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EFFECT OF TEMPERATURE ON THE BIOLOGICAL PARAMETERS OF APHIS CRACCIVORA (HEMIPTERA APHIDIDAE) ON ROBINTIA PSEUDOACACIA

Borowiak-Sobkowiak B. – Effect of temperature on the biological parameters of Aphis craccivora (Hemiptera Aphididae) on Robinia pseudoacacia.

Aphis craccivora is considered to be a potential indicator for global warming. This species is characterized by a fast developmental rate and a high reproductive potential. It reveals a number of adaptation strategies to adjust to changing environmental conditions. The paper presents the impact of temperature on developmental stages, fecundity, survival rate and the demographic parameters of A. craccivora rear on Robinia pseudoacacia. The research was carried out under control at five constant temperatures of 10, 15, 20, 25, and 28°C, 75% humidity and photoperiod 16 L:8 D. The higher the temperature, the shorter the observed length of the pre-reproductive period, ranging from 6 days at 28°C up to 24 days at 10°C. The intrinsic rate (\(r_m\)) was maximal (0.42) at 28°C and minimal (0.07) at 10°C. With increasing temperature, the impact of environmental factors on the population growth potential is no information on the impact of different constant temperatures on the demographic growth parameters of cowpea aphids on trees. This paper fills this gap in the literature.

Net reproductive value (\(R_o\)) informs about the average number of offspring that a female produces during her lifetime. Data concerning the daily fecundity enable one to foresee the size of population (Southwood, 1966). Net reproductive rate is also significant in indicating the quality of the host plant and the ability of a female to produce the progeny (Bernardi et al., 2012).

Aphis craccivora Koch is one of the most significant crop pests worldwide, causing large losses of harvest (Minks and Harrewin, 1987; Blackman and Eastop, 2000). It settles on over 50 plant species from 19 families (Mehrparvar et al., 2012). It is most numerous on plants of the Fabaceae family, settling on both herbaceous plants and trees (Heie, 1986). It can settle the following genera: Lupinus, Medicago, Melilotus, Trifolium, Vicia, Caragana and Robinia. It is a serious pest in vegetable farming and one of the most serious pests for cowpea, Vigna unguiculata (L.) in the tropical regions and for peanut crops in Africa and in Pakistan.

It is also one of the few aphid species that has been assigned a trophic status (Jaba et al., 2010). This species is characterized by a fast rate of development and a high reproductive potential. It also shows a range of adaptation strategies to adjust to changing environmental conditions, especially high temperatures (Borowiak-Sobkowiak et al., 2017). Aphis craccivora may be a potential indicator for global warming, because of their lower temperature threshold for growth than other aphid species (Kuo and Chen, 2004).

Thus far, many papers have been concerned with studying the impact of temperature on A. craccivora on herbaceous plants (Berg, 1984; Kuo and Chen, 2004; Chen et al., 2009; 2013; Sofjan and Aldawood, 2014). However, there is no information on the impact of different constant temperatures on the demographic growth parameters of cowpea aphids on trees. This paper fills this gap in the literature.
MATERIALS AND METHODS

APHID SOURCE

*Aphis craccivora* were collected from *Robinia pseudocacia* L. in Poznań in 2015 by the author. The collected females were transferred to the laboratory where the aphids were reared on plant seedlings to produce large colonies which would constitute the material for further research. The material was deposited in Department of Entomology and Environmental Protection, at the Poznań University of Life Sciences.

EXPERIMENTAL PROCEDURES

Aphids were reared on 25-30 cm-long seedlings of *Robinia pseudocacia*. The plants were put in pots and watered twice a week. The experiment was carried out at five different temperatures: 10°C, 15°C, 20°C, 25°C, 28°C, and at 75% humidity and photoperiod of L:D = 16:8 in a climate chamber (Sanyo).

For each experimental temperature, 20, young, apterous adult aphids of the same age were each individually placed on shoots. The length of the following developmental stages was recorded: pre-reproduction, reproduction, post-reproduction, total life span and female fecundity. The observations were carried out six times per week.

To determine the demographic parameters of populations, 100 larvae were observed. At each temperature, 30 females were introduced onto each plant. One-day-old larvae born by the females were recorded for the experiment. In order to calculate the total fecundity of the population and the mean fecundity of the female, the newly born larvae were counted and removed. Observations were taken five times per week. Demographic parameters for *Aphis craccivora* populations at five different temperatures were determined according to the methods described by Birch (1948). The net reproduction rates (Ro), the mean generation time (T), the intrinsic rate of increase (rm), the finite rate of increase (λ), the time necessary for the population to double (DT), were calculated. The intrinsic rate (rm) was calculated using the WYATT and WHITE formula (1977): \( r_m = 0.738 \left( \frac{\ln M_d}{d} \right) \), where d is the developmental period from birth to the beginning of the first reproduction and M_d is the number of nymphs born in the period from time d. The net reproduction rate is given by \( R_o = \sum (m_l) \), where m_l and m represent cumulative daily survival and fertility respectively; mean generation time \( T = \ln R_o/r_m \); the finite rate of increase \( \lambda = e^{r_m} \) and doubling time \( DT = \ln 2/r_m \).

DATA ANALYSIS

All data were analysed using an ANOVA, using StatSoft Inc.’s, Statistica, version 9.0.

Statistical analyses evaluated the data for specific developmental stages of generations, total lifespan and fecundity at different temperatures. A linear regression analysis was used to estimate the lower developmental threshold for aphids analysing the developmental rate data obtained at constant temperatures from 10°C to 28°C. On the basis of the regression equation, the number of degree-days necessary for development at the lower developmental threshold was calculated.

RESULTS

The research indicates that temperature has a significant influence on the development of *Aphis craccivora* (Fig. 1, Table 1). As temperature increased, the duration of the pre-reproductive period decreased, ranging from an average of 24 days at 10°C to 6 days at 28°C. Differences were observed, in particular between the periods of larvae development at 10°C, 15°C, and 28°C (Fig. I, 1).

The rate of nymph stage of development was positively and linearly related to increasing temperature. The highest rate of development was observed at a temperature of 28°C. Based on the regression equation \( y = 0.064x^2 - 0.0213, \quad R^2=0.9679 \), the threshold temperature for development is 3.3°C (Fig. II).

The higher the temperature, the shorter the duration of the reproductive period. The mean duration of the reproductive period ranged from approximately 29 days at 15°C and 20°C, to approximately 14 days at 28°C. The duration of the reproductive period of females at 10°C and at 25°C was similar, yet differed significantly from the reproductive period of females reared at 28°C (Fig. I, 2). The post-reproductive period ranged from an average of 1 day at 25°C to as many as 10 days at 10°C (Fig. I, 3). The total longevity of aphids ranged from 24 to 61 days (Fig. I, 4). The shortest lifespan was registered for specimens living at a temperature of 28°C and the longest – at 10°C. The lifespan of aphids reared at 15–25°C temperatures differed significantly from the lifespan of females reared at 10°C and 28°C. *A. craccivora* females are characterized as displaying high fecundity (Fig. I, 5), dependent on the temperature. The smallest number of larvae was delivered by females at 10°C (on average 20 larvae per female), while the highest fecundity was observed in females reared at 20°C (on average 115 larvae per female) (Table 1). A growth in female fecundity was registered with increasing temperature up to 20°C, following which aphid fecundity gradually decreased. The fecundity of aphids reared at 10°C significantly differed from the fecundity of aphids reared at other temperatures.

*A. craccivora* is characterized by high larvae survival (Fig. III). As much as 100% of larvae reaches maturity at 20°C, while the highest mortality is observed at 28°C. Associated with the change of temperature there were differences in the number of larvae born by females during the day (Fig. IV). The highest daily fecundity was registered on the 8th day of life for females developing at 28°C (about 9 larvae/female).

Intrinsic rate (\( r_m \)) achieved its maximal value (0.42) at 28°C and minimal value (0.07) at 10°C (Table 2). From the calculated population demographic parameters it follows that during the day the population of *A. craccivora* on *R. pseudocacia* increased from (I) 1.08 to 1.53 times with increasing temperature. The mean time for a single generation to develop (T) ranged from 9.81 days at 28°C up to 37.04 days at 10°C. The population (\( R_o \)) increased from 14.93 to 109.02 times as temperature increased up to 20°C, and then subsequently decreased (Table 2).

The research has demonstrated that the most conducive development strategy for *A. craccivora* occurs at 28°C. At this temperature, the species reaches maturity the fastest and its population evinces the highest \( r_m \) parameter.

DISCUSSION

The results of the presented research indicate that temperature has a substantial effect on the biological parameters of *A. craccivora*. With increasing temperature the pre-reproductive period was found to decrease. At a temperature of 28°C the observed developmental time
from birth to reproduction for this species on *R. pseudoacacia* was only 6 days. Similar results were observed for *A. craccivora* on alfalfa at 23.9°C (BERBERET et al., 2009), on subterranean clover at 21°C (GUTIERREZ et al., 1971) and on broad bean at 20°C (TRACIEVSKI and WARD, 1994). Research results by KUO and CHEN (2004) differ from those presented above, the authors stating that the developmental time of immature *A. craccivora* reared on asparagus bean at 30°C was 4.2 days. The research findings of many authors indicate that the developmental rate for *A. craccivora* is not influenced by the host plant on which it settles (BERBERET et al., 2009). However, rapid larvae development leads to an increase in the number of generations and favours more numerous aphid colonization of plants. The length of the pre-reproductive period is also connected with the level of resistance or sensitivity of plants. A high level of plant resistance causes a prolonging of the pre-reproductive period in insects, in comparison with susceptible cultivars (OBOPILE and OSTILE, 2010).
Fig. II – Rate of development (1/day) of larval stage of apterous *Aphis craccivora* as a function of temperature $y = 0.0064x - 0.0213$, $R^2 = 0.9679$.

Fig. III – Survival rates of apterous *Aphis craccivora* at different temperatures.

Fig. IV – Fecundity of apterous *Aphis craccivora* at different temperatures.
The developmental threshold for *A. craccivora* on *R. pseudoacacia* in this study was estimated to be 3.3°C. This means that at this temperature the developmental time for this species from 1st instar to adult is high and amounts to 156.25 dd. This parameter is much lower than the one offered by GUTIERREZ et al. (1971) for aphid populations reared in Australia on forage legume species (8.3°C), by KUO and CHEN (2004) in Taiwan for *A. craccivora* on asparagus bean (7.4°C), or by BERBERET et al. (2009) on alfalfa in Oklahoma (7.1°C). These research findings correspond with the theory that a geographically separated population of aphids can differ in terms of the extent of temperature tolerance and population growth rates (MEHRPARVAR and HATAMI, 2007).

Temperature had a significant impact on the reproduction and fecundity of aphids. The rate of reproduction appeared to be the key determinant in the aphid’s population growth rate (BERG, 1984). The results of this study indicate that a temperature range of 15 to 25°C is optimal for reproduction of *A. craccivora* on *R. pseudoacacia*. The species, reared in these temperatures, can reproduce from 64% to 77% of its longevity respectively. These research findings correspond with the research of BERBERET et al. (2009). The authors confirm that temperatures ranging from 18-24°C are optimal for reproduction of *A. craccivora* on alfalfa, on which females give birth to 82 larvae on average. BERG (1984), however, states that *A. craccivora* is known to indicate a greater population growth potential at 25°C.

Aphids reared on *R. pseudoacacia* are characterized by high fecundity, reaching their maximum at 20°C (on average 115 larvae/female). Such high fecundity of *A. craccivora* has not been noted on other plants. KUO and CHEN (2004) observe 97.1 larvae per female on asparagus bean at 26°C. GUTIERREZ et al. (1971) on *Trifolium repens* 98, on *Medicago polymorpha* 93 nymphs per female at 21°C, TRACIEVSKI and WARD (1994) 90 nymphs on broad bean at 20°C, while SOFFAN and ALDAWOOD (2014) 41 to 65 nymphs on faba bean at 26°C.

High fecundity was also observed in *A. craccivora* females reared at 15, 25 and 28°C. The highest, daily, female fecundity was usually observed at the beginning of the reproduction period with 7 and 9 larvae per female observed at 20°C and 28°C respectively. This confirms the general assumption that the progeny are supposed to peak at the beginning of the reproduction period (WYATT and WHITE 1977).

Temperature significantly influences aphid longevity leading to it prolonging its lifespan as the temperature drops. *A. craccivora* on *R. pseudoacacia* lived three times shorter at 28°C than those reared at 10°C. Longevity did not negatively affect fecundity of females reared at higher temperatures. For most aphid species, a temperature of 20-22°C is optimal for their development. *Aphis craccivora* can develop even in much higher temperatures. According to KUO and CHEN (2004), at 35°C this species reaches maturity but its longevity and fecundity become significantly limited. As a result of global warming, high numbers of aphid nymphs are likely to survive to adulthood, but most adults could fail to reproduce (CHEN et al., 2013). The authors predicted that *A. craccivora* longevity and reproduction would decrease as the summer temperatures increased, based on the hypothesis that climate warming will eventually exceed their physiological optima.

According to DIXON (1987) the developmental rate of aphids within the range between the lower and upper threshold temperatures is usually linear. These results confirm this theory. However, those by MEHRPARVAR and HATAMI (2007), DURAK and BOROWIAK-SOBOKWI (2013) indicate that the relationship between the development and temperature is non linear at the extremes of an aphid’s physiological tolerance.

This research also highlights the impact of temperature on the demographic parameters of *A. craccivora* on *R. pseudoacacia*. The intrinsic rate of increase grows with the increase in temperature. This coefficient reaches its maximal value at 28°C. The finite rate of increase also grows with increasing temperature, while the average time of generation development shortens. Yet the net reproductive value reaches its maximum at 20°C. Apart from mean generation time, all demographic parameters of *A. craccivora* on black locust are higher than those recorded for *A. craccivora* on asparagus bean (KUO and CHEN 2004), or on seven different cowpea cultivars studied by HAIFZ (2006). It shows that *R. pseudoacacia* is a good host plant for *A. craccivora*. The intrinsic rate of natural increase differed significantly between varieties, dependent on their resistance level. OBOPILE and OSITILE (2010), studying the population parameters of cowpea aphid on five *Vigna unguiculata* varieties, obtained a higher $r_n$. Their results indicate that studies of life tables and population dynamics are useful tools in characterizing aphid resistance in crop plants. This research confirms that the growth of temperature will continue to have a positive impact on this species’ population growth and will make this aphid not only a pest to herbal plants but also to trees. *A. craccivora* is a species of high migrating potential and can adjust to new environmental conditions and new plants.

The research suggests that the optimal range of temperatures for the development of *A. craccivora* on *R. pseudoacacias* is 20-28°C, which corresponds with the findings of KUO and CHEN (2004). Within these temperatures, the species typically has a short pre-reproductive period, high fecundity and the highest rate of population growth. Aphids have the potential to respond rapidly to climate change as a result of their short generation time and high fecundity (HARRINGTON et al., 1995). *Aphis craccivora* is considered to be a potential indicator for global warming because of its lower threshold temperature for growth (KUO and CHEN, 2004). At the present time the importance of heat-tolerant species has increased, as the role of some tends to increase and of others – decrease (JAWORSKI and HILSZCZANSKI, 2013). Thus, in the future, together with global warming, *Aphis craccivora* may become more problematic. Finding out

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**Table 2 – Life table parameters describing *Aphis craccivora* as a function of temperature.**

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>$R_0$</th>
<th>$R_m$</th>
<th>$\lambda$</th>
<th>$T$</th>
<th>$DT$</th>
</tr>
</thead>
<tbody>
<tr>
<td>10</td>
<td>14.93</td>
<td>0.07</td>
<td>1.08</td>
<td>37.04</td>
<td>9.49</td>
</tr>
<tr>
<td>15</td>
<td>90.43</td>
<td>0.21</td>
<td>1.23</td>
<td>21.45</td>
<td>3.3</td>
</tr>
<tr>
<td>20</td>
<td>109.02</td>
<td>0.3</td>
<td>1.35</td>
<td>15.43</td>
<td>2.28</td>
</tr>
<tr>
<td>25</td>
<td>71.52</td>
<td>0.28</td>
<td>1.32</td>
<td>15.19</td>
<td>2.47</td>
</tr>
<tr>
<td>28</td>
<td>63.4</td>
<td>0.42</td>
<td>1.53</td>
<td>9.81</td>
<td>1.64</td>
</tr>
</tbody>
</table>

$R_0$ = net reproductive rate; $R_m$ = intrinsic rate of increase; $\lambda$ = finite rate of increase; $T$ = generation time; $DT$ = doubling time.
about aphid developmental changes in reaction to global warming matters in ecology and plant protection. It is therefore crucial to carry out further research concerning the impact of temperature on aphid development as well as research connected with integrated methods of plant protection against A. craccivora.

ACKNOWLEDGEMENTS

I would like to express my gratitude to Magdalena Płachecińska and Bernadeta Wielgus for their help in conducting research.

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