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The grapevine aphid, *Aphis illinoisensis*: thermal requirements for development and its performance on six grapevine cultivars

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Abstract

The grapevine aphid, *Aphis illinoisensis* (Shimer), has invaded various regions in the Mediterranean basin. The aim of this study was to determine the thermal requirements for aphid development and to assess its performance on six grapevine cultivars of economic importance in Greece. The grapevine aphid was reared at four constant temperatures (17 - 26 °C) on 'Soultanina' and 'Agiorgitiko' cultivars and the thermal summation method was applied to estimate the lower developmental thresholds and the thermal constants in each cultivar. In addition, age-specific life tables were constructed and population growth parameters on cultivars 'Soultanina', 'Savvatiano', 'Moscato Bianco', 'Agiorgitiko', 'Mavrodafni' and 'Merlot' were estimated at 23 °C. Our data revealed that aphids develop faster with increasing temperatures within the 17 - 26 °C range on both cultivars. The theoretical lower developmental threshold was 4.2 °C and 5.4 °C and 110.9 and 104.1 day-degrees were required for aphids to reach adulthood on 'Soultanina' and 'Agiorgitiko', respectively. Mean adult longevity and mean post-reproductive period varied significantly among cultivars. Aphids lived significantly longer on 'Savvatiano' than on 'Moscato Bianco', 'Soultanina' and 'Mavrodafni', and the longest post-reproductive period were recorded for aphids reared on 'Savvatiano', 'Agiorgitiko' and 'Merlot'. However, mortality and developmental rates, mean lifetime fecundity and population growth parameters didn't differ significantly among grapevine cultivars. Overall, our data showed that all examined cultivars are suitable hosts for the aphid. This study is the first dealing with the development and population growth of *A. illinoisensis* related to temperature and the results contribute to better understanding the biology of the species and improve pest management practices.

Key words: Aphididae, day-degrees, demography, developmental threshold, viticulture.

Introduction

The grapevine aphid, *Aphis illinoisensis* (Shimer), is a North American species (Baker, 1917; Blackman and Eastop, 2006) that has recently invaded Mediterranean regions. It was first recorded in Turkey (Remaudière *et al.*, 2003; 2006) and then in Greece (Tsitsipis *et al.*, 2005; 2007). Up to now, it has been also recorded in Tunisia (Kamel-Ben Halima and Mdellel, 2010), Algeria (Laamari and Coeur d'acier, 2010), Montenegro (Petrović-Obradović *et al.*, 2010) and Israel (Barjadze and Ben-Dov, 2011).

A. illinoisensis is a pest of grapevines, forming colonies both on young terminal shoots and on the lower side of young leaves (Blackman and Eastop, 2006). In case of high population levels, the aphid might feed on fruit clusters causing some grape berries to drop (Pfeiffer and Schultz, 1986). In North America, the grapevine aphid is assumed to be a host-alternating holocyclic species. The species has one sexual generation on *Viburnum prunifolium* L. (Caprifoliaceae) in autumn and several parthenogenetic (all-female) generations on several secondary hosts (genera of Vitaceae, including *Ampelocissus*, *Cissus*, *Parthenocissus*, *Vitis*) during summer (Baker, 1917; Blackman and Eastop, 2006). However, there is no evidence of sexual forms of *A. illinoisensis* in Turkey, Greece and Montenegro (Remaudiere *et al.*, 2003; Tsitsipis *et al.*, 2005; Margaritopoulos *et al.*, 2009; Petrović-Obradović *et al.*, 2010). In preliminary laboratory experiments, aphids from the island of Crete, Greece, failed to produce sexual forms after being reared for three consecutive generations under short day conditions (L10:D14) at 17 °C (Tsamandani, unpublished data). The warm climate of the aforementioned countries may allow the aphid to reproduce parthenogenetically all year, enhancing the establishment of asexual invasive genotypes. However, there have not been yet recorded alternative hosts during the winter period when grapevines do not possess any foliage on which the aphids feed on. Accordingly, much research is needed to clarify whether the grapevine aphid is able to reproduce sexually in the Mediterranean regions which have been invaded recently. As far as virus transmission is concerned, the grapevine aphid has not been reported to be a vector of grapevine viruses (Kuniyuki *et al.*, 1995), but it is capable of transmitting *Watermelon mosaic virus*-2 (WMV-2) (Adlerz, 1987; Webb *et al.*, 1994).

Numerous invasive phytophagous insect species from North America have succeeded in establishing permanent populations in Europe, owing partly to similarity in climatic conditions (Coeur d'acier *et al.*, 2010). Apart from the temperate climate, the presence of suitable hosts is also essential for their successful establishment in continental Europe. In Greece, *A. illinoisensis* was first recorded in the island of Crete (Tsitsipis *et al.*, 2005) and it has been thus far distributed in most of the viticultural regions of the mainland (Margaritopoulos *et al.*, 2009). The viticultural regions of Greece, being located all over the country, are characterized by a mosaic of noir, rose and white cultivars which are expected to have an impact on growth and reproductive rates of grapevine aphid. Indeed, host cultivar quality, being partly associated with their secondary metabolites, plays a decisive role in insect fitness (Awmack and Leather, 2002; Klemola *et al.*, 2007). In case that the grapevine cultivars grown in Greece are suitable for rapid development and sufficient population growth of the invasive aphid, this species might pose a threat to Greek viticulture. Accordingly, data on aphid development and population growth could be useful to determine the pest status of the species and to improve future control programs.

Up to now, there is no published data both on thermal requirements for the grapevine aphid development and on life table parameters on different grapevine cultivars (*Vitis vinifera* L.). Thus, the aims of the present study were: i) to determine the thermal requirements for development of the recently introduced in Greece grapevine aphid, and ii) to assess the aphid performance on six grapevine cultivars of primary economical importance for Greek viticulture.

Materials and methods

Plant material

Three white (Soultanina, Savvatiano and Moscato Bianco) and three noir (Agiorgitiko, Mavrodafni and Merlot) grapevine cultivars were used for the performance tests (table 1). The selected cultivars are of economic importance in Greece and exhibit genetic similarity with many other Greek and economically important cultivars of other countries (Lefort and Roubelakis-Angelakis, 2001; Crespan and Milani, 2001; Hvarleva *et al.*, 2005).

The plant material used was certified and virus-free, grafted on cuttings of American rootstocks (110 R, 1103 P.) and they were provided by Vitro Hellas S.A. (Alexandria Imathias, Greece). The grafted material was rooted in a mixture of soil substrate 'Primo' (Plantaflor Company, Germany) and perlite (2:1) in pots under controlled greenhouse conditions. Plants were maintained at 25 - 20 °C day/night temperature, 50 - 60% RH, and ambient light. The pots were watered twice a week and no fertilization was applied. Plants at the two-to-four-leaf stage of development were used in experiments.

Insects

In the summer of 2005, *A. illinoisensis* individuals were collected from grapevines on the island of Crete, Greece, where the aphid was first recorded in the country. A parthenogenetic lineage of the aphid was established on a different cultivar than those used in the performance trials and maintained in a bioclimatic chamber at controlled conditions (23 ± 1 °C, 60 ± 5% RH and a photoperiod of L16:D8) in the Laboratory of Entomology and Agricultural Zoology of the University of Thessaly, Volos, Greece. The aphid lineage was reared for several consecutive generations on grapevine plants until the beginning of the experiments.

Thermal requirements for development

Experiments were conducted at four constant temperatures (17, 20, 23 and 26 °C), with 60 ± 5% RH and 16:8 L:D photoperiod in controlled environment rooms. Randomly selected apterous adult females from the stock culture were placed on the cultivars 'Soultanina' and 'Agiorgitiko'. Three to five females were used for each plant and the experiment was conducted in 10 replications (plants) per cultivar at each temperature regime. Females were free to choose their feeding sites and allowed to reproduce for 24h, and then they were removed. The newborn nymphs (40 - 117 depending on the cultivar and temperature treatment) were observed daily and their survival was recorded until they produced their first nymph. The number of days from birth to the onset of reproduction was recorded and the percent nymphal mortality was calculated. Each plant with the newborn nymphs was covered with a PVC cage with tulle in order to prevent them from escaping, infesting other plants or being exposed to parasitization.

Performance tests

Experiments were conducted at 23 ± 1 °C, 60 ± 5% RH, L:D 16:8h in a controlled environment room. Two adult females were randomly selected from the stock colonies and transferred to each examined cultivar by a fine camel's hair brush. They were allowed to reproduce for 24h and then the adults were removed. The survival rate of the newborn nymphs (56 - 59 per cultivar) was recorded daily until reaching the adult stage. At the same time, two adult females were randomly selected from the stock colonies and transferred to each plant of

Table 1. Characteristics and geographical distribution of the grapevine cultivars used in the performance tests. Vigour is the quality or condition that is expressed in rapid growth of the parts of the vine; it refers essentially to the rate of growth.

Grapevine cultivar	Berry colour	Main areas of cultivation	Time of grape maturation	Vigour
Soultanina	white	Peloponnesus and Crete island	early	yes
Savvatiano	white	Sterea Greece, Thessaly, Macedonia, Peloponnesus	late	yes
Moscato Bianco	white	Samos island, Peloponnesus	early	no
Agiorgitiko	noir	Peloponnesus, Eastern Sterea Greece	late	yes
Mavrodafni	noir	Peloponnesus, Ionian island	late	no
Merlot	noir	Western Macedonia, Peloponnesus	early	yes

the examined cultivars by a fine camel's hair brush. Thirty plants (replicates) per examined cultivar were used, being covered with a PVC cage with tulle to prevent escape and parasitism. Adults were allowed to reproduce for 24h and then all adults and their newborn nymphs were removed from each experimental plant, except for one nymph. The number of days from birth to the onset of reproduction was recorded for each cultivar. Adults remained free to choose feeding sites on the plants and the offspring born and adult survival were recorded daily. All newborn nymphs were removed after they were recorded. Observations continued until all parent aphids were dead in each cultivar. Adult longevity, lifetime fecundity and duration of adult reproductive and post-reproductive periods were calculated for each cultivar.

Statistical analysis and life tables

The normality of data was assessed by the Kolmogorov-Smirnov test (Chakravarti *et al.*, 1967). In case the structure of the data did not meet normality assumptions, non-parametric methods were used to compare means.

Non-parametric Kruskal-Wallis tests were used to assess the effect of temperature on developmental time in 'Soultanina' and 'Agiorgitiko' cultivars while the effect of the aforementioned cultivars on developmental time of aphid in each temperature regime was examined using non parametric Mann-Whitney U-tests. Nymphal mortality between varieties and temperature treatments was compared using χ^2test.

A linear regression analysis was applied to the developmental points within 17 - 26 °C range to compute the lower development threshold of the grapevine aphid by using developmental rate and temperature treatment as dependent and independent variable, respectively. The lower developmental threshold was determined as the x-intercept of the linear equation and the degree-day requirements were determined as the value of the inverse of the linear equation slope. According to the 'thermal summation' method (Messenger, 1964), the linear relationship between temperature and the developmental time is expressed by the equation $D \times (T - T_0) = K$, where D is the developmental time at a certain temperature T, T_0 is the 'developmental zero' and K is the 'thermal constant' (day-degrees).

As far as performance tests are concerned, variation in mean developmental time of aphid on the six grapevine cultivars was examined using non-parametric Kruskal-Wallis test and non-parametric chi-square analysis was applied to assess the effect of cultivar on nymphal mortality. Kaplan-Meier estimators of adult longevity, reproductive period and post-reproductive period were calculated for each cultivar. Pairwise comparisons of the respective periods between cultivars were conducted using the log rank (Mantel-Cox) test. The structure of the data on lifetime fecundity meets normality and assumptions of parametric statistics. Lifetime fecundity, as affected by cultivar source (first factor) and the time interval between measurements (repeated factor), was inferred using a repeated measure analysis of variance (ANOVA).

Population growth rates of aphid on six grapevine cultivars were calculated from Lotka equation (Birch, 1948): $1 = \Sigma e^{-rm \times x} l_x \times m_x$, in which x = age in days (including immature stages), r_m = intrinsic rate of increase, l_x = age specific survival (including immature mortality) and m_x = age specific number of female offspring. After computing r_{all} for all aphids in each examined cultivar, the jackknife method was used to estimate the variance of r_m-values (Meyer *et al.*, 1986). The jackknife pseudo-value $r_{m(j)}$ was calculated for the n samples using the following equation: $r_{m(j)} = n \times r_{all} - (n - 1) \times r_i$. Moreover, the net reproductive rate $R_0 = \Sigma l_x m_x$, mean generation time $GT = \ln R_0 / r_m$, mean doubling time $DT = \ln 2 / r_m$, and mean finite rate of increase $\lambda = e^{rm}$ were estimated for each cultivar (Birch, 1948). Non-parametric Kruskal-Wallis tests were used to assess the effect of the grapevine cultivar on net reproductive rate, mean generation time, mean doubling time and mean intrinsic rate of increase. The statistical analyses were conducted by the SPSS v.17.0.1 statistical package (SPSS Inc. Chicago, IL, U.S.A).

Results

Thermal requirements for development

Temperature affected significantly aphid mortality on 'Agioritiko' cultivar (χ^2 = 20.9; df = 3; P < 0.001) but not on 'Soultanina' cultivar (χ^2 = 6.8; df = 3; P = 0.079) with the highest rate observed at 26 °C (42.7%). In the case of 'Agiorgitiko', two among the six possible pairwise comparisons between temperature treatments were found significant, i.e. 26 vs. 23 °C (42.7 vs. 11.4%; χ^2 = 14.0; χ^2 critical value = 7.0; d.f. = 1; P < 0.05) and 26 vs. 17 °C (42.7 vs. 19.2%; χ^2 = 11.6; χ^2 critical value = 7.0; d.f. = 1; P < 0.05). Significant differences between cultivars were found in two temperature treatments. Mortality was higher on 'Agiorgitiko' than 'Soultanina' at 26 °C (42.7 vs. 15.3%; χ^2 = 17.3; d.f. = 1; P < 0.001) whereas the opposite was observed at 23 °C (11.4 vs. 30.0%, χ^2 = 4.5; d.f. = 1; P = 0.034) (table 2). The mean time required by the nymphs to reach adulthood significantly decreased with increasing temperature on both 'Soultanina' (K-W: χ^2 = 151.6; df = 3; P < 0.001) and 'Agiorgitiko' (K-W: χ^2 = 197.3; df = 3; P < 0.001) (table 2). Cultivar had no significant impact on developmental time within each temperature regime, except for the lowest temperature examined where aphids developed significantly faster on 'Soultanina' than on "Agiorgitiko' (17 °C: U = 750.0, n = 103, P < 0.001; 20 °C: U = 1026.0, n = 98, P = 0.273; 23 °C: U = 447.0, n = 67, P = 0.121; 26 °C: U = 2271.0, n = 139, P = 0.438). The estimated developmental thresholds and thermal requirements of grapevine aphid reared on 'Soultanina' and 'Agiorgitiko' are 4.2 °C and 5.4 °C and 110.9 and 104.1 day-degrees, respectively (table 3). Thermal requirements for aphid development were slightly different between the examined grapevine cultivars.

Performance on six grapevine cultivars

Mortality rates of nymphs ranged from 3.4% ('Maurodafni') to 14.6% ('Agiorgitiko') and were not significantly affected by grapevine cultivar (χ^2 = 7.5; df = 5; P = 0.183).

Table 2. Developmental time and nymphal mortality of *A. illinoisensis* reared on 'Soultanina' and 'Agiorgitiko' at four constant temperatures and L:D 16:8h.

Temperature (°C)	Soultanina Nymphal mortality[(1)] (%)	N	Agiorgitiko Nymphal mortality[(1)] (%)	N	Soultanina Developmental time, (days) mean ± SE[(2)]	N	Agiorgitiko Developmental time, (days) mean ± SE[(2)]	N
17	13.0 aA	46	19.2 aA	78	8.30 ± 0.1 a	40	8.90 ± 0.9 b	63
20	27.3 aA	55	29.3 aAB	82	7.45 ± 0.9 a	40	7.33 ± 0.8) a	58
23	30.0 aA	40	11.4 bA	44	5.89 ± 0.9 a	28	5.69 ± 0.8 a	39
26	15.3 aA	85	42.7 bB	117	5.03 ± 0.7 a	72	5.12 ± 0.6 a	67

[(1)]Mortality rates within rows followed by different small letter and within columns by different capital letter are significantly different ($P < 0.05$, χ^2 test).
[(2)]Within rows, means followed by different letter are significantly different ($P < 0.05$, Mann-Whitney test).

Table 3. Regression values a and b [$R(T) = a + bT$], developmental thresholds ($T_0 = - a / b$) and thermal requirements ($DD = 1 / b$) of *A. illinoisensis* reared on 'Soultanina' and 'Agiorgitiko'.

Grapevine cultivar	Regression values a	b	R^2	Developmental threshold, T_0 (°C)	Thermal requirements in day-degrees, K
Soultanina	−0.0382	0.0090	0.9737	4.2	110.9
Agiorgitiko	−0.0517	0.0096	0.9846	5.4	104.1

Table 4. Adult longevity and post-reproductive period (mean ± SE, n = 30) of *A. illinoisensis* reared on six grapevine cultivars at 23 °C and L:D 16:8h.

Grapevine cultivar	Parameters, mean ± SE Adult longevity (days)	Post-reproductive period (days)
Soultanina	19.50 ± 0.39 a	6.83 ± 0.43 a
Savvatiano	23.83 ± 0.51 c	9.57 ± 0.60 b
Moscato Bianco	19.70 ± 0.36 a	7.30 ± 0.46 a
Agiorgitiko	21.57 ± 0.59 b	8.83 ± 0.62 b
Mavrodafni	19.33 ± 0.43 a	6.20 ± 0.38 a
Merlot	21.30 ± 0.60 b	9.23 ± 0.47 b

Within columns, means followed by the same letter are significantly different ($P < 0.05$, log rank test).

Mean developmental time (5.57 - 5.87 days) didn't differ significantly among the examined grapevine cultivars (K-W: $\chi^2 = 7.856$; df = 5; $P = 0.164$). Mean adult longevity, ranging from 19.3 to 23.8 days, differed significantly among the grapevine cultivars (Log rank test (Mantel-Cox): $\chi^2 = 46.9$, df =5, $P<0.001$). Adults reared on 'Savvatiano' were the longest lived, as opposed to adults on 'Soultanina', 'Moscato Bianco' and 'Mavrodafni' (table 4). In contrast, mean reproductive period (11.40 - 13.57 days) did not differ among the grapevine cultivars examined [Log rank test (Mantel-Cox): $\chi^2 = 8.7$, df = 5, $P = 0.124$]. Also, mean post-reproductive period of aphids was significantly affected by the grapevine cultivar [Log rank test (Mantel-Cox): $\chi^2 = 39.2$, df = 5, $P < 0.001$]. Aphids reared on 'Savvatiano', 'Agiorgitiko' and 'Merlot' remained alive after ceasing reproduction for a significant longer period than on the other cultivars. Moreover, mean lifetime fecundity (58.63 – 64.37 nymphs) did not differ among the grapevine cultivars examined (Repeated Measures ANOVA, $F = 1.3$, df = 5. $P = 0.270$; $df_{Error} = 171$).

Age specific survival rates were high up to adult day 20 for aphids reared on the examined grapevine cultivars, except for 'Savvatiano' wherein survival rates remained high until adult day 24 (figure 1). Then there was a sharp decrease until death. The age patterns of reproduction were similar among the grapevine cultivars. Peak oviposition rates were recorded between the ages of 8 and 11 days (days after birth), when more than 7 aphids were produced by the average female followed by a rapid decrease in reproduction (figure 1). In addition, grapevine cultivar caused no significant variation in net reproductive rate of adults (R_0 = 49.6 - 60.5 females/female/generation) (K-W: $\chi^2 = 9.1$, df = 5, $P = 0.104$), mean generation time (GT = 8.2 - 8.6 days) (K-W: $\chi^2 = 7.1$, df = 5, $P = 0.212$), mean doubling time (DT = 1.39 – 1.50 days) (K-W: $\chi^2 = 4.6$, df = 5, $P = 0.465$) and mean intrinsic rate of increase (r_m = 0.468 – 0.498 females / female/ day) (K-W: $\chi^2 = 4.1$, df = 5, $P = 0.536$).

Discussion and conclusions

Our data showed that the developmental rate of *A. illinoisensis* increases linearly within the range of 17 - 26 °C on both 'Soultanina' and 'Agiorgitiko' without considerable variation between cultivars at temperatures above 20 °C. The examined temperature range can be considered as suitable for aphid development, supporting its abundance throughout the slightly warm springs of Mediterranean areas. However, developmental rates of aphids are restricted by high temperatures that are close to upper developmental threshold (Wang and Tsai, 2000; Mehrparvar and Hatami, 2007). Indeed, infesta-

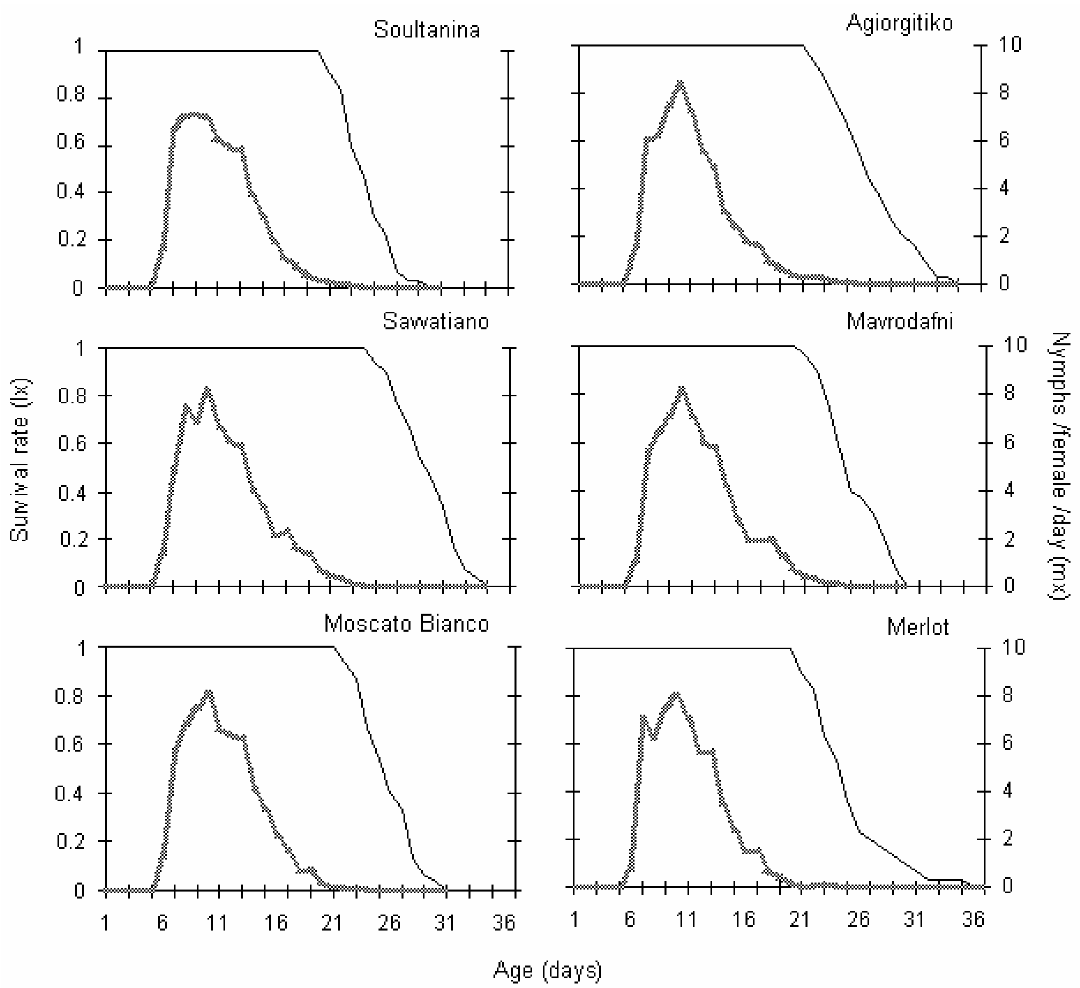

Figure 1. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *A. illinoisensis* on six grapevine cultivars at 23 °C and L:D 16:8h (n = 30). Solid and grey lines denote survival rate and reproductive rate, respectively.

tion level of the vineyards on the island of Crete were found to be reduced during the warm summer period (Tsitsipis *et al.*, 2005), suggesting that the development of grapevine aphid is probably restricted by high temperatures and the mature stage of grapevine leaves.

In addition, we found that the thermal requirements for grapevine aphid development (≈ 110 day-degrees) are close to those of species that generally prefer warm temperate climate, such as *Aphis gossypii* Glover (Kersting *et al.*, 1999), *Brevicoryne brassicae* (L.) (Raworth, 1984) and *Rhopalosiphum* species (Elliott *et al.*, 1988; Elliott and Kieckhefer, 1989), albeit the grapevine aphid begins to develop at 1 - 2 °C lower than the above species. It is noted that the low developmental threshold of the grapevine aphid is more than 1 °C lower on 'Soultanina' than 'Agiorgitiko', being probably adapted to spurting status of cultivars in the spring. Field experiments are required to ascertain these relatively low temperature requirements. Nonetheless, species being abundant in early season or cooler temperatures, such *Acyrthosiphon pisum* (Harris), are capable of developing at substantial lower temperatures (2.4 °C) and need more thermal units (150 day-degrees) until adult development than the grapevine aphid (Siddiqui *et al.*, 1973).

Taking into account that the 'thermal constant' is characteristic of a species (Messenger, 1964), the estimated values of thermal constant and developmental zero for the grapevine aphid can be used for predicting aphid appearance in Greek viticulture areas. However, laboratory data should be cautiously applied in field in order to make phenological predictions (Bergant and Trdan, 2006). In our case, for instance, working with young plants might limit the extent of the findings because older plants develop more or less the physical leaf characteristics that can affect aphid development. Also, it should be noted that temperature range within which linear model can be applied is usually restricted to 15 - 30 °C (Campbell *et al.*, 1974) and thus inclusion into analysis too low or too high temperatures would lead to underestimation of developmental zero and thermal constant. Despite being an approximate model, the linear model is broadly used due to its simplicity, the minimal data required for formulation, its quite adequate predictions for aphid development within the optimum range and the adaptive ecological significance of its parameters (Kipyatkov and Lopatina, 2010).

Performance of aphid species has been reported to vary greatly among host-plants (Tsai and Wang, 2001; Yoo *et al.*, 2005; Goławska, 2010; Takalloozodeh, 2010) and cultivars (Razmjou *et al.*, 2006; Silva *et al.*, 2006; Zarpas *et al.*, 2006; Bayhan, 2009; Obopile and Ositile, 2010). In the present study, there was no significant variation in nymphal mortality, developmental rates and lifetime fecundity of *A. illinoisensis* among the examined cultivars, as opposed to adult longevity and duration of post-reproductive period. In particular, aphids reared on 'Savvatiano' were the longest lived while post-reproductive period was significantly longer for aphids reared on 'Savvatiano', 'Agiorgitiko' and 'Merlot' compared to the other cultivars. Nonetheless, the life table parameters of the grapevine aphid didn't differ significantly among grapevine cultivars. The intrinsic rate of increase that is presumed to be as the most informative mean of evaluating host-plant suitability did not differ significantly among grapevine cultivars. Combined with the short developmental time and the remarkable total reproduction, the suitability of all the examined grapevine cultivars as host plants is outlined.

Various studies have shown that leaf morphology affects aphids' survival and performance (Legrand and Barbosa, 2000; Zarpas *et al.*, 2006; Buchman and Cuddington, 2009). The abaxial leaf surface of both 'Savvatiano' and 'Mavrodafni' is considered as pilose, as opposed to glabrous status of 'Soultanina' leaves, and leaves from 'Merlot' have a rugose surface. Nonetheless, our results show that the morphological differences of the examined grapevine cultivars are not capable of causing variation in grapevine aphid development and in the life-table parameters examined. This could be partially attributed to the fact that aphids were free to choose the most suitable feeding sites and thus they were able to avoid possible resistance factors related to leaf morphology and/or mature stage of leaves.

Overall, this is the first study to deal with *A. illinoisensis* development and population growth. Our developmental rate model supports that the prevailing climatic conditions throughout spring period in the Mediterranean regions in general, and in particular in Greece, are favourable for the grapevine aphid development. In addition, all the examined grapevine cultivars were found to be suitable host-plants. Consequently, the data presented here combined with evidence for asexual mode of reproduction, which promotes high levels of population increase, outline the potential pest status of the grapevine aphid in Greece, particularly where aphid ensures its survival throughout winter.

Though life table studies under constant temperatures are useful in understanding the population dynamics of insect pests (Summers *et al.*, 1984), future research efforts should focus on the effects of additional and/or fluctuating temperatures on grapevine aphid population growth. In this context, population parameters could be used as bioclimatic indices in assessing the potential of the aphid population growth in new viticulture areas. It is worth mentioning, however, that more aspects of the grapevine aphid bio-ecology in the Mediterranean basin need to be elucidated. For instance, detailed studies on the life-cycle category and the genetic structure of the invasive populations should be conducted, although current evidence suggests asexual mode of reproduction, along with extended surveys for winter or alternative hosts, presumably close-related to grapevine.

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