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Temperature-dependent life history of *Schizaphis graminum* on barley

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Abstract

A population of greenbug, *Schizaphis graminum* (Rondani) was originally collected from barley fields in Isfahan (central Iran). Biology and thermal requirements were studied on the barley plants (Karoon variety) under laboratory conditions at seven constant temperatures: 10, 15, 19, 22, 26, 31, and 33 ºC, 60 ± 5% RH, and a photoperiod of 16:8 L:D. The aim of this study was to evaluate the effect of temperature on biology and development with thermal requirement of the greenbug on barley (Karoon variety). Developmental time decreased significantly from 32 to 6 days as the temperature increased from 10 to 26 ºC and then increased to 10.18 days at 31 ºC. The aphid failed to develop at 33 ºC. Survivorship of immature stages varied from 88% at 26 ºC to 27% at 31 ºC. The highest and lowest longevity were observed at 10 and 26 ºC, respectively. The aphids doubling time and mean generation time were significantly higher at 10 ºC (12.19 ± 0.02 and 38.70 ± 0.35 days, respectively). The r_m ranged from 0.06 at 10 ºC to 0.31 at 26 ºC. The lower developmental threshold was 5.73 ºC and the aphids required 133.33 degree-days (DD) to complete the immature life cycle. The results of this study showed that 26 ºC is optimal temperature for greenbug development and growth.

Key words: greenbug, development, demography, thermal requirement, Iran.

Introduction

The greenbug, *Schizaphis graminum* (Rondani) (Hemiptera Aphididae) is thought to be palearctic in origin and is now found in North, Central and South America, Europe, Africa, the Middle East and Asia (Blackman and Eastop, 2000). The host range of greenbug includes 70 grasses (Teetes and Pendleton, 2000). Among the reported cereals pests, greenbug could produce significant damage on cereals by feeding on the phloem and injecting toxic salivary enzymes that induce chlorosis around the feeding site (Pendleton *et al.*, 2009). Also, *S. graminum* can transmit several important viruses, it being the most effective vector of barley yellow dwarf virus in several varieties of *Hordeum vulgare* L. (Poaceae) (Rezvani, 2001). Severe infestation of cereals by the greenbug usually occurs every 5-6 years resulting in cyclical high pesticide use (Pedigo, 1995). The greenbug usually colonize in early growing spring and winter grains in the central part of Iran (Rezvani, 2001).

Temperature is a key factor influencing aphid development. Geographically separated populations, of aphids may differ with respect to the effect of temperature on developmental rates (Campbell *et al.*, 1974; Razmjou *et al.*, 2006). The net reproductive rate, fecundity, intrinsic rate of increase, and developmental threshold are variables essential to describe the temperature effects on aphid population growth (McCornack *et al.*, 2004). Geographical region, species, population, and developmental stage affect thermal characteristics as well (Gilbert and Raworth, 1996; Roy *et al.*, 2002; 2003).

To develop an IPM program for this species, an exact determination of population parameters is required. No other data are available on demography and thermal requirements of greenbug in Iran. The objective of this study was to determine thermal requirements and relationship between temperature and greenbug's development and reproduction. These characteristics are used to predict population levels and thermal adaptation of this aphid.

Materials and methods

Host source and colony maintenance

Seeds of barley (Karoon varietry) were obtained from the Karaj Cereal Research Department of the Iranian Research Institute of Plant Breeding and sown in standard mixed soil in 15 cm diameter pots. The greenbugs used in this study were originally collected from barley fields in Isfahan central part of Iran in March 2008. The stock culture of aphids was established on Karoon barley in climate chambers at 22 ± 1 ºC, 60 ± 5% RH., and a photoperiod of 16:8 L:D. The aphids were reared on barley for four generations before using them in the experiments. Every week, aphids were transferred from infested plants to the youngest ones to maintain the colony. The same seedlings were used for all experiments.

Nymphal development and survival

The aphids were cultured at each tested temperature for one generation before using them in the experiments. For each temperature, 100 young apterous adult females (less than 24 h old) were transferred on experimental plants for nymph production. After four hours, adults were removed and 85 newly emerged nymphs were collected and used under seven constant temperatures including 10, 15, 19, 22, 26, 31, and 33 ± 1 °C, 60 ± 5% RH., and a photoperiod of 16:8 L:D. Clear plastic clip cages (6 cm-diameter) were used for the experiments. A 3cm-diameter hole was cut in the centre of the cups and covered with fine mesh cloth for ventilation. Clip cages were attached to the stem and primary leaf of the same seedlings. After that each nymph was transferred individually on experimental host plants using a camel's-hair brush and caged with a clip cage to estimate their developmental time. Experimental aphids were monitored daily for ecdysis. The survivorship and moulting was recorded every 24 hours. In these experiments, the population failed to survive at 33 ºC, therefore, this temperature was excluded from the data analysis.

Adult longevity and reproduction

Newly emerged adult's reproduction and longevity were studied at six constant temperatures (50 replications for each temperature) until the last female died. The number of offsprings produced by each female and the survival of apterous adults were recorded every 24 hours. The fresh host plants were provided every 3 days during the course of the experiments.

Data analyses

All data of developmental time, longevity and stable population growth parameters were analyzed for each temperature by using Proc GLM of SAS statistical package (SAS Institute, 1988). From the fertility and survivorship schedules, the following population growth parameters were calculated using formula suggested by Carey (1993): intrinsic rate of increase (r_m), mean generation time (T_c), finite rate of increase (λ), net reproduction rate (R_o) and doubling time (d_t). Differences in R_o, T_c, λ, d_t and r_m-values were tested for significance by estimating variances through the Jackknife technique (Meyer *et al.*, 1986, Maia *et al.*, 2000). Algorithm for jackknife is described only for r_m. similar procedures were used for the other parameters (R_o, T_c, λ and *dt*). The jackknife pseudo-value r_j was calculated for the *n* samples using the following equation:

$$r_j = n \times r_{all} - (n - 1) \times r_i$$

After calculating all the *n* pseudo-values for r_m, jackknife estimate of the mean [$r_{m(Jackknife)}$ or $r_{m(J)}$], variance and standard error calculated by the following equations:

$$r_{m(J)} = \frac{\sum_{i=1}^{n} psv\, r_{m(i)}}{n}$$

$$\mathrm{var}(r_{m(J)}) = \frac{\sum_{i=1}^{n} \left(psv\, r_{m(i)} - r_{m(J)}\right)^2}{n-1}$$

$$SE(r_{m(J)}) = \sqrt{\frac{\mathrm{var}\left(r_{m(J)}\right)}{n}}$$

The mean values of *n* jackknife pseudo-values for each temperature were subjected to analysis of variance (ANOVA) (Kersting *et al.*, 1999). The similar procedures were used for the other parameters such as R_o, λ, *T* and *DT*. If significant differences were observed, multiple comparison were made using LSD.

The relationship between temperature and the developmental rate was described using linear regression:

$$Y = a + bx,$$

where *Y* is the developmental rate, *x* is the temperature, *a* is the intercept and *b* is the slope of the line.

The degree-day (DD) was obtained for different stages of the greenbug aphid using the following formula: DD = 1 / *b*. The lower developmental threshold (T_o) was calculated using the following relationship: T_o = -a / b (Campbell *et al.*, 1974).

Results and discussion

Effect of temperature on developmental time

The period of immature development of *S. graminum* on the Karoon variety of barley at six constant temperatures is summarized in table 1. The total developmental time for *S. graminum* decreased from 32.72 days at 10 ºC to 6.65 days at 26 ºC. When the temperature was increased from 10 to 26 ºC, aphid development decreased significantly, but increased to 10.18 days at 31 °C. The effect of temperature on developmental time, mortality, fecundity, life history parameters and degree day for this species and another aphid species have been presented by many authors (Bowling *et al.*, 1998; Morgan *et al.*, 2001; Satar and Yokomi, 2002; Zamani *et al.*, 2006). But no other study has examined the detailed effects of temperature on demography and the pre-adults thermal requirements of *S. graminum* on barley in Iran.

The greenbug successfully developed to adulthood from 10 to 31 ºC, but no development accrued at 33 ºC, thus we believe that this can be considered as an upper lethal temperature. These results were in agreement with those obtained by Tofangsazi (2009) for the greenbug on other barley cultivars. Development rate is near zero at the low temperature threshold, increases with temperature and levels off at the optimum, and then decreases rapidly as the high threshold is approached. This relationship is curvilinear near the extremes, but approximately linear at moderate temperatures (Wagner *et al.*, 1984). The developmental period of the first instar aphid was slightly longer than other nymphal instars at all tested temperatures. This is in agreement with Walgenbach *et al.* (1988) at temperature range of 11-29 ºC when the aphid fed on barley. At this period of life, the nutrition of the first instar nymph is very low; therefore, they need a longer time for ecdysis so the developmental period will increase. The optimal developmental time of the greenbug was estimated at 26 ºC (6.65 ± 0.08 days) and it was significantly shorter than other evaluated temperatures.

The lower developmental threshold (T_o) and degree day (DD) values estimated for *S. graminum* at all immature stages showed significant differences ($P < 0.05$) (table 2). The lower developmental threshold varied from 4.33 ºC for the 1st nymphal instar to 7.48 ºC for the 4th instar nymphs. Furthermore, the highest value of the thermal requirement was estimated for the 1st instar nymphs in comparison to other immature stages. Aphids need 133.33 degree-days for development from birth to adult. There is a significant correlation between devel-

Table 1. Developmental time of *S. graminum* at six constant temperatures.

Growth instars	Temperature (°C)					
	10	15	19	22	26	31
1^{st} instar	9.10 ± 0.17[a]	4.23 ± 0.07[b]	3.41 ± 0.06[c]	2.61 ± 0.07[d]	2.26 ± 0.05[e]	4.25 ± 0.10[b]
2^{nd} instar	8.04 ± 0.21[a]	3.54 ± 0.01[b]	2.23 ± 0.08[cd]	1.87 ± 0.07[ed]	1.66 ± 0.06[e]	2.28 ± 0.08[c]
3^{rd} instar	7.86 ± 0.15[a]	3.31 ± 0.08[b]	2.12 ± 0.07[cd]	1.79 ± 0.06[d]	1.48 ± 0.06[e]	2.42 ± 0.09[c]
4^{th} instar	7.60 ± 0.18[a]	3.13 ± 0.07[b]	2.39 ± 0.08[c]	1.76 ± 0.07[d]	1.22 ± 0.08[e]	2.18 ± 0.10[c]
Preimaginal development	32.72 ± 0.41[a]	14.20 ± 0.11[b]	10.11 ± 0.11[c]	8.23 ± 0.11[d]	6.65 ± 0.08[e]	10.18 ± 0.22[c]

Means with the same letters in each row are not significantly different by LSD test (P = 0.05).

Table 2. Linear regression of developmental rates (*Y*) and temperature (*x*) for immature stages of *S. graminum*.

Growth instars	Lower developmental threshold (T_0) (ºC)	Degree day (DD)	Linear regression models	R^2	*P*-value
1^{st} instar	4.33	50.00	Y = −0.0902 + 0.0208x	0.98	0.98
2^{nd} instar	5.59	32.15	Y = −0.1741 + 0.0311x	0.98	0.98
3^{rd} instar	6.13	28.73	Y = −0.2135 + 0.0348	0.99	0.99
4^{th} instar	7.48	24.21	Y = −0.3093 + 0.0413x	0.96	0.96
Preimaginal development	5.73	133.33	Y = −0.043 + 0.0075x	0.99	0.99

R^2: Coefficient of determination.

opmental time and temperature for all immature stages, with r^2 values ranging from 0.96-0.99. Total developmental time for total immature stages is estimated 7.22 ± 0.10 days at 26 ºC for *Sitobion avenae* (F.) fed on barley (Kieckhefer *et al.*, 1989), which was higher than that reported in this study (6.65 ± 0.08 days). Lee *et al*., (2007) estimated that the upper developmental temperature for greenbug was 32.5 ºC which was relatively similar to that obtained in this study (between 31 and 33.5 ºC).

The linear regression for the developmental rate in relation to temperature is Y=0.043+0.0074X, where *Y* is developmental rate and *X* is temperature (figure 1). The lower developmental threshold for total immature stages was 5.73 ºC which was close to 5.86 ºC for the same species on barley, however the estimated degree-day for development of total immature stages in this study (133.33 degree-day) was higher than 93.19 degree-day reported by Walgenbach *et al.* (1988). The lower developmental threshold and degree-day were reported 6.8 ºC and 109 degree-day by Lee *et al*. (2007), which were higher and lower, respectively, than those obtained in this study. The first instar nymphs seem to be the most tolerant to low temperature due to their lowest estimation of thermal thresholds. Regarding to the regression line slope, a positive correlation was observed between developmental rate and studied temperature range (10-26 ºC).

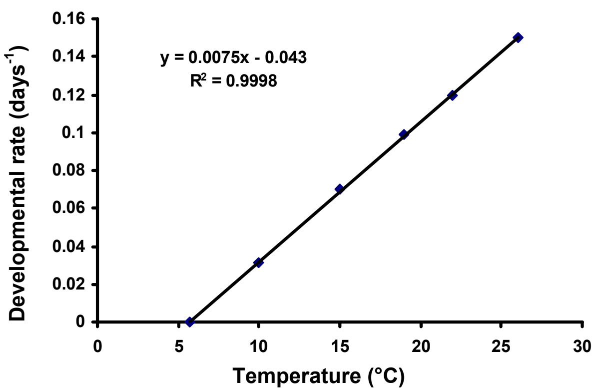

Figure 1. Developmental rate (1/development time) for total immature stages of *S. graminum* at different temperatures.

Survival and fecundity

The highest and lowest percentage of nymphal survival were observed at 26 ºC (88%) and 31 ºC (27%), respectively. The survival rate at the temperatures of 10, 15, 19 and 22 ºC were 55%, 70%, 76% and 85%, respectively. The age specific survival at all six temperatures decreased with increasing the aphid age, and most of the mortality occurred late in the life (adult stage). At temperatures of 10 and 31 ºC, most of the mortality occurred early in the lifespan. In fact aphid's survivorship decreased more rapidly to zero at the lower and upper temperatures. In contrast, at other temperatures (15, 19, 22 and 25 ºC), most of the mortality occurred late in the lifespan. The lowest survival and fecundity were observed at 31 ºC (figure 2). Similar decrease in survivorship for *A. gossypii* at the same temperatures has previously been reported by Zamani *et al*. (2006).

Age-specific fecundity curves vary depending on temperatures. The maximum fecundity rate was calculated at 22 ºC (5.02 nymphs/ female/ day). The fecundity for *S. graminum* tended to be low at the beginning of the reproductive period at all experimental temperatures. The maximum peak of reproduction was observed at 26ºC. The similar pattern of fecundity and lower range of total number of nymphs per female (9.7- 60.1) was reported for *Acyrthosiphon pisum* (Harris) on pea (Morgan *et al*., 2001).

Longevity and reproduction capacity

Adult longevity and total number of offspring per female for the greenbug are given in table 3. Adult longev-

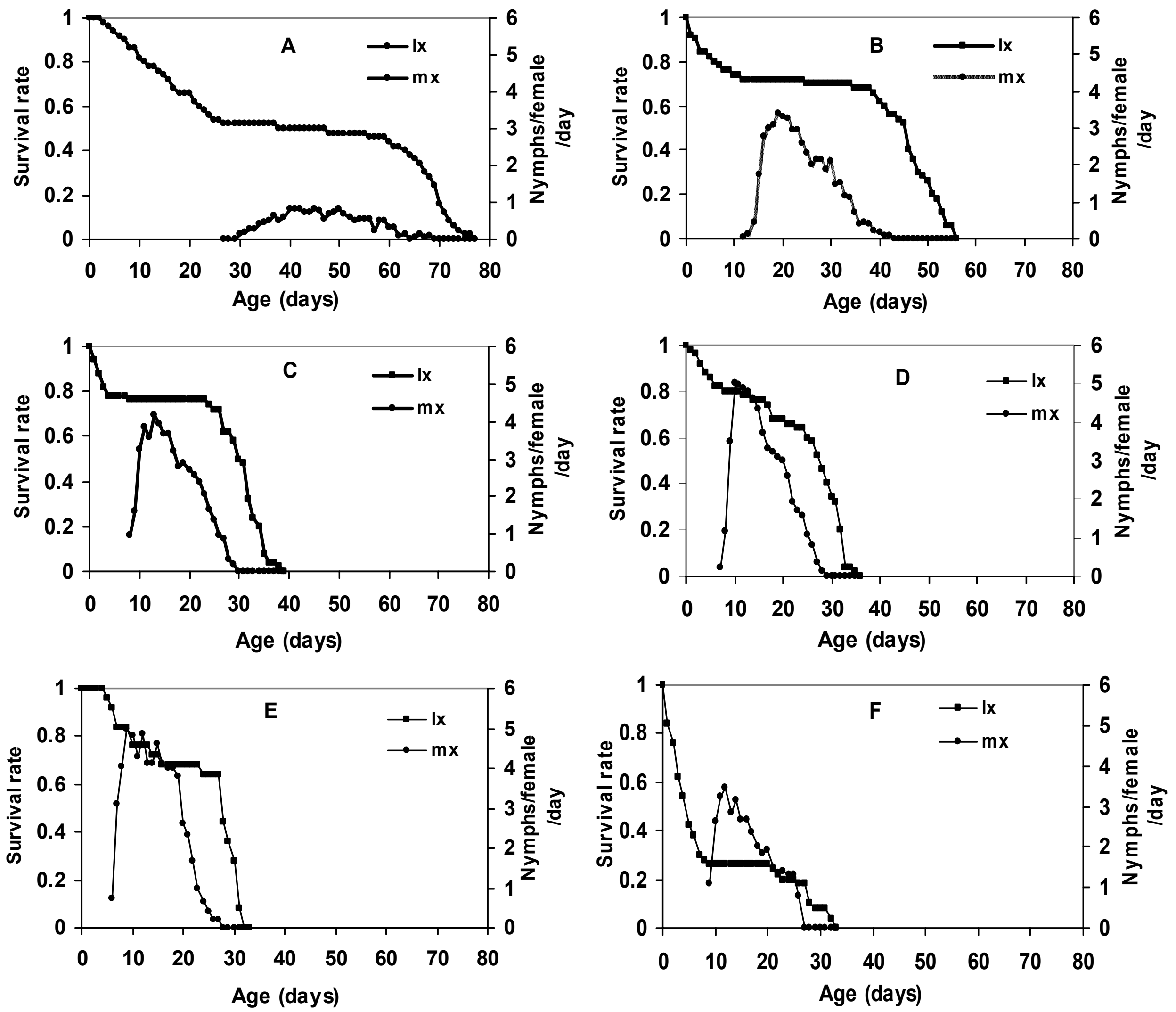

Figure 2. Age-specific fecundity and survivorship for *S. graminum* reared at (A) 10 ºC, (B) 15 ºC, (C) 19 ºC, (D) 22 ºC, (E) 26 ºC, and (F) 31 ºC on barley (Karoon variety), l_x is the proportion of alive aphids at age *x*; m_x *is* the mean number of nymphs laid per female at age *x*.

Table 3. Mean longevity (days ± SEM) and mean number of offspring per female (± SEM) of *S. graminum* at six constant temperatures.

Temperature (ºC)	Longevity	Total no. of nymphs/ female
10	66.23 ± 0.89[a]	16.38 ± 0.60[d]
15	46.24 ± 0.85[b]	47.90 ± 1.36[b]
19	30.88 ± 0.63[c]	50.22 ± 1.43[b]
22	30.37 ± 0.85[cd]	54.31 ± 1.78[b]
26	25.36 ± 1.56[cd]	66.14 ± 3.47[a]
31	27.87 ± 1.02[e]	34.09 ± 1.62[c]

Means with the same letters in each column are not significantly different (P = 0.05).

ity decreased with increasing temperature from 10 to 26 ºC, but this parameter increased at 31 ºC. The longevity of the greenbug was determined between 25.36 to 66.23 days in this study. This is relatively similar with those reported by Pendleton *et al*. (2009) for greenbug biotype I (8.6 to 61.9 days) reared on Sorghum. The mean total number of nymphs per female was highest at 26 ºC (66.14 ± 3.47) and lowest at 10 ºC (16.38 ± 0.60). There was an adverse correlation between longevity and total number of nymphs per female. The greatest number of nymphs per female and shortest longevity was obtained at 26 ºC, which showed it is the best temperature for greenbug population growth.

Life table parameters

The life table parameters for *S. graminum* at six constant temperatures are given in table 4. Temperature strongly affected some demographic parameters of *S. graminum*. The calculated r_m, R_o and λ values increased by increasing temperature from 10 ºC to 26 ºC but those values decreased at 31 ºC. The intrinsic rate of increase (r_m) ranged from 0.06 at 10 ºC to 0.31 at 26 ºC, respectively. The calculated R_0 and λ values significantly differed at various temperatures and the highest estimates were observed at 26 ºC (57.89 ± 2.87 and 1.37 ± 0.01, respectively). The mean generation time (T_c) and dou-

Table 4. Comparison of life history parameters of *S. graminum* at six constant temperatures (n = 50).

Temperature (ºC)	Parameters (mean ± SEM)				
	Net reproductive rate (R_0)	Intrinsic rate of increase (r_m) (d^{-1})	Generation Time (T) (days)	Doubling time (days)	Finite rate of increase (λ) (d^{-1})
10	9.77 ± 0.30[d]	0.06 ± 0.00 [d]	38.70 ± 0.35 [a]	12.19 ± 0.02[a]	1.05 ± 0.00 [e]
15	37.32 ± 1.15 [c]	0.19 ± 0.02 [c]	20.00 ± 0.25 [b]	3.83 ± 0.07 [b]	1.19 ± 0.00 [d]
19	40.06 ± 0.92 [c]	0.26 ± 0.00[b]	13.89 ± 0.16 [c]	2.62 ± 0.02 [c]	1.30 ± 0.00[c]
22	47.33 ± 1.17[b]	0.29 ± 0.00 [ab]	13.01 ± 0.17 [cd]	2.37 ± 0.02 [c]	1.33 ± 0.00 [b]
26	57.89 ± 2.87[a]	0.31 ± 0.00 [a]	12.27 ± 0.25 [d]	2.17 ± 0.05 [c]	1.37 ± 0.01 [a]
31	9.76 ± 0.31[d]	0.16 ± 0.00 [c]	13.44 ± 0.26 [c]	4.19 ± 0.09 [b]	1.21 ± 0.03 [d]

Means with the same letters in each column are not significantly different (P = 0.05).

bling time (D_t) had the lowest values at 26 ºC (12.27 ± 0.25 and 2.17 ± 0.05, respectively).

The greenbug achieved the highest r_m and R_o at 26 ºC because of their highest m_x and shorter developmental time. These values were higher than those reported by Nuessly *et al.* (2008) for greenbug fed on *Paspalum vaginatum* Swartz (0.23 and 12.3, respectively). Decreasing R_o and r_m values at 10 and 31 ºC suggests that low and high temperatures affect aphid development, survival, and reproduction. The mean generation time and doubling time were significantly higher at the lowest temperature (10 ºC) and decreased by increasing the temperature from 10 to 26 ºC. The mean generation time and doubling time followed the same trend for *A. gossypii* on cucumber at 10 to 25 ºC (Zamani *et al.*, 2001). The highest and lowest values of finite rate of increase were obtained in population reared at 26 ºC and 10 ºC, respectively, similar to those reported by Kieckhefer *et al.*, (1989) for *S. avenae* reared on the same host plant (λ = 1.012 - 1.014). According to the whole estimated population growth parameters, the optimum temperature for the greenbug outbreaking seems to range between 22-26 ºC close to 22.5-25 ºC reported by Satar and Yokomi (2002) for *B. schwartzi* on peach. The population growth parameters may be affected by ecotypical differentiation, geographical region, host plants, and experimental condition.

Temperature is one of the most important factors influencing aphids biology (Kieckhefer *et al.*, 1989). Several reports have been published on the effect of temperature on the life history of greenbug on different host plants (Walgenbach *et al.*,1988; Nuessly *et al.*, 2008; Lee *et al.*, 2007; Penteldon *et al*, 2009;), but no data are available on the Iranian population of this aphid. This study indicates that temperature plays a significant role in population's dynamics of this aphid through its influence on immature development, survival and reproduction. The foregoing results clearly demonstrate that *S. graminum* has the potential to achieve high population densities in spring and winter barley fields early in growing season in our experimental region. There is a possibility that some changes in planting and harvesting dates of barley could reduce the aphid's damage in moderate climate regions of Iran. Nevertheless, further research on their biology, thermal requirements and evaluation of the intrinsic rate of increase under the field condition at moderate climate areas are needed.

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