

Temperature-dependent life history of *Sipha maydis* (Hemiptera: Aphididae) on wheat

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Abstract: *Sipha maydis* (Passerini) is a pest of Poaceae in many cereal-growing area of the world and Iran. The effects of temperature on biology and life table were investigated at five constant temperatures (15, 20, 25, 30 and 32.5±1°C), 60±5% relative humidity (RH) and a photoperiod of 16L : 8D h. The results indicated that aphids failed to complete development at 32.5°C. Developmental time was ranged between 17.28 to 9.55 days at 15 and 30°C, respectively. The lower developmental threshold (T_0) and thermal constant of *S. maydis* were estimated to be -5.52°C and 332.22 degree-days, respectively. The Analytis-3/Briere-1 model (as non linear model) is highly recommended for the description of temperature dependent development of *S. maydis*. The highest life expectancy of adults at emergence was 33.35 days at 20°C. The mean adult longevity of females and nymphositional period were the highest at 20°C. The mean lifetime fecundity at 15, 20, 25 and 30°C were 21.24±1.97, 44.82±3.18, 22.25±2.33 and 16.39±1.15 nymphs/female, respectively. The survivorship curves of *S. maydis* were type I at 20 and 25°C ($H < 0.5$) and type III at 15 and 30°C ($H > 0.5$). The highest and lowest values of intrinsic rate of increase (r_m) were observed at 20 (0.173±0.012 females/female/day) and 15°C (0.109±0.003 females/female/day), respectively. The growth index (GI) at 15, 20, 25 and 30°C were 0.033, 0.069, 0.062 and 0.038, respectively. According to this research the optimum temperature for population growth of *S. maydis* was 20°C. Our findings provide fundamental information and when this information is used in association with other ecological data, it may be valuable in development and implementation of management programs of *S. maydis*.

Key words: cereal aphid, development, demographic parameters, Iran

Introduction

Cereal aphids are problem in agricultural ecosystems (Vickerman and Wratten 1979). *Sipha maydis* (Passerini) living mainly on a wide range of wild grasses and cereal crops and it has been reported on 30 genera of Gramineae (Imwinkelried *et al.* 2004; Blackman and Eastop 2006). It is distributed in Europe, central and middle Asia, North and South Africa (EI-Yamani and Hill 1991) and has recently distributed in Argentina (Delfino 2002; Ortego *et al.* 2004). This aphid has significant damage on youngest leaves of wild grasses and cereals sown early in autumn and mature cereal plants in late spring. The *S. maydis* feeds on the upper surface of leaf, ligula region of flag leaves, ears and sometimes on the stem and inflorescences (Saluzzo 2004; Blackman and Eastop 2006; Corrales *et al.* 2006) and it can transmit several important viruses such as cucumovirus (*Cucumber mosaic virus*) and luteovirus (*Barley yellow dwarf virus*) (EI-Yamani and Hill 1991; Blackman and Eastop 2000). It has been shown that *Rhopalosiphum padi* (Hemiptera: Aphididae) play an important role in the epidemiology of certain diseases, such as Barley Yellow Dwarf (BYD) on winter barley in Poland (Strażyński 2011). Heavily infested plants often become yellowed, rolled into tubes and desiccated (Blackman and Eastop

2000). It is an economically important pest of all cereal crops in drier climates (Blackman and Eastop 2000).

Climate and weather variables such as temperature have effect on aphid phenology and population growth rate (Walters and Dewar 1986; Andreev *et al.* 2009). Population mortality depends upon several interrelated factors such as snow, precipitation and temperature (Armstrong and Peairs 1996). Among these variables, temperature has the most impact (Huffaker *et al.* 1999). However, many intrinsic characteristics of plants such as nutritional value, secondary chemicals and morphology can influence the fecundity, growth and survival of insect herbivores (Goławska 2010). Host plant quality is also known to be an important factor affecting aphid demography, survival, fecundity and life expectancy (Rostami *et al.* 2012).

The entomopathogenic fungus *Lecanicillium longisporum* (Hypocreales: Ascomycota) is recently reported as a capable alternative control agent against *S. maydis* (Fadayivata *et al.* 2014).

Mathematical models such as linear and nonlinear models have been used to explain insect development rates and estimate various critical temperatures (Campbell *et al.* 1974; Logan *et al.* 1976; Lactin *et al.* 1995; Briere *et al.* 1999).

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In the literature, no other studies are available on the effect of temperature on demographic parameters and thermal requirements of *S. maydis*. The objective of this study was to determine thermal requirements and relationship between temperature and *S. maydis* development and reproduction.

Materials and Methods

Insect culture

Population of *S. maydis* used in this research was originally collected from wheat fields at the College of Agriculture of Tarbiat Modares University (Tehran, Iran) during September 2009. The stock culture of aphids was established on Pishtaz wheat in a growth chamber at temperature of $25 \pm 1^\circ\text{C}$, $60 \pm 5\%$ relative humidity (RH) and a photoperiod of 16L : 8D (Light : Dark) h.

Experimental conditions

The aphids were cultured at each tested temperature for one generation before using them in the experiments. For each temperature, 50 young apterous adult females (less than 24 h old) were transferred individually on wheat leaves into 1.5 ml micro tube and placed in BD Falcon™ 50 ml conical centrifuge tubes (<http://www.bdbiosciences.com/cellculture/tubes>). After 24 h, adults were removed and only one newly born nymph was maintained on each 10 days-old wheat seedling to develop. Developmental stages of *S. maydis* were checked daily and survival and mortality of different stages was separately recorded. When the immature nymphs become adults, they were observed daily for reproduction and survival and all new-born nymphs were counted and removed from each leaf cage. The experiments were continued until the death of all individuals of the cohort in all temperatures. To reduce the effects of plant age on reproduction and survivorship, aphids were carefully transferred on new wheat leaves every 4–5 days.

The experiments were conducted at 15, 20, 25, 30 and $32.5 \pm 1^\circ\text{C}$, $60 \pm 5\%$ RH and a photoperiod of 16L : 8D h.

Statistical analysis

The data of the number of female progeny and survival of *S. maydis* were used for the estimation of different life table parameters. Their calculations were conducted by the following equations (Carey 1993, 2001):

– the age-specific survival rate (l_x):

$$l_x = \frac{N_x}{N_0},$$

– life expectancy (e_x):

$$e_x = \frac{T_x}{l_x},$$

– entropy parameter (H):

$$H = \frac{\sum_{x=0}^{\omega} e_x d_x}{e_0}, \quad d_x = l_x - l_{x+1},$$

– net reproductive rate (R_0):

$$R_0 = \sum_{x=\alpha}^{\beta} l_x m_x,$$

– intrinsic rate of natural increase (r_m):

$$1 = \sum_{x=1}^{\omega} e^{-rx} l_x m_x,$$

– mean generation time (T):

$$T = \frac{\ln R_0}{r_m},$$

– doubling time (DT):

$$DT = \frac{\ln 2}{r_m},$$

– finite rate of increase (λ):

$$\lambda = e^{r_m},$$

where: x – the age in days, l_x – probability to survive from birth to the beginning of age class x , N_x – number of surviving females entering age class x , N_0 – the initial number of individuals in the cohort, e_x – life expectancy at age x , T_x – the number of time units lived by the cohort from age x until the death of all cohort individuals. Also, growth index (GI) computed as the ratio between the percentage of adults emerged and the duration of the immature period (Ramasubramanian and Babu 1989). If $H < 0.5$, $= 0.5$ or > 0.5 , the survival schedule would be convex, linear and concave, respectively. If $H = 0$, then all deaths occur at exactly the same age and if $H = 1$, then the shape of survival schedule exponentially declining, e is the base of natural logarithms, β – the maximum age among the n individuals, α – the pre-imaginal development time, m_x – mean number of female progeny per female of age class x .

After r_m was computed for the original data ($r_{m(\text{all})}$), the jackknife method was applied to evaluate the differences in r_m values by estimating the variances. The jackknife pseudo-value $r_{m(i)}$ was estimated for the n samples by using the following formulae (Meyer *et al.* 1986; Maia *et al.* 2000):

$$PSVr_{m(i)} = n \times r_{m(\text{all})} - (n-1) \times r_{m(i)},$$

$$r_{m(\text{mean})} = \frac{\sum PSVr_{m(i)}}{n},$$

$$VARr_{m(\text{mean})} = \frac{\sum_{i=1}^n (PSVr_{m(i)} - r_{m(\text{all})})^2}{n-1},$$

$$SEMr_{m(\text{mean})} = \frac{\sqrt{VAR(r_{m(\text{mean})})}}{n},$$

where: PSV – pseudo-value, VAR – variance, SEM – standard error of the mean.

This method was used for the other parameters (R_0 , λ , T and DT). Statistical analysis was carried out using SAS

(SAS Institute 2003) and MINITAB software (MINITAB 2000). The differences in population parameters were compared using one-way analysis of variance (ANOVA). If significant differences were detected, multiple comparisons were made using the Student-Newman-Keuls (SNK) ($p < 0.05$) with SPSS 16 (SPSS 2004).

The linear regression model was used to evaluate the lower developmental threshold (T_0) and the thermal constant (K) for the overall immature period of *S. maydis*. The model of Campbell *et al.* (1974) is based on the linear regression equation:

$$r(T) = a + bT,$$

where $r(T)$, is the developmental rate and T is the temperature ($^{\circ}\text{C}$). The parameters a and b , are the intercept and the slope of the straight line, respectively. The lower temperature threshold is calculated as $T_0 = -a/b$ and the thermal constant as $K = 1/b$.

Also, six non-linear models were used to explain the effect of temperature on the development of *Diuraphis noxia* (Mordvilko) (Table 1). Estimated parameters of non-linear models were accomplished using JMP software (SAS Institute 2007).

The goodness of fit of each model assess based on coefficient of determination (R^2), adjusted coefficient

of non-linear regression (R^2_{adj}) and the residual sum of squares (RSS). The Akaike information criterion (AIC) (Akaike 1974) is another goodness-of-fit parameter is calculated by equation (Vucetich *et al.* 2002):

$$AIC = n \ln(SSE/n) + 2p,$$

where: n – the number of temperatures, p – the number of measurable parameters of each model, SSE – the sum of standard error.

Results

Relationship between temperature and developmental time

S. maydis females successfully developed into adults at temperatures ranging from 15 to 30 $^{\circ}\text{C}$. At 32.5 $^{\circ}\text{C}$, only 18% of newly born aphid reached to the third nymphal instar but all of them died during the fourth instar. The effect of temperature on the development of *S. maydis* is shown in table 2. Temperature had significant effect on aphid developmental time ($F = 164.592$; $df = 3, 122$; $p < 0.05$). Developmental time was ranged between 17.28 \pm 0.33 to 9.55 \pm 0.26 days at 15 and 30 $^{\circ}\text{C}$, respectively. The first instar nymphs need a longer time than other nymphal instars to complete developmental period at all tested temperatures (Table 2).

Table 1. Non-linear models of regression used to describe the effect of temperature on the development of *S. maydis*

Models	Name	Reference
$r(T) = \psi \left[e^{\rho T} - e^{\left(\rho T_{\max} - \tau \right)} \right], \quad \tau = \frac{T_{\max} - T}{\Delta T}$	Logan-6	Logan <i>et al.</i> (1976)
$r(T) = a \left[\frac{1}{1 + K e^{-\rho T}} - e^{-\tau} \right], \quad \tau = \frac{T_{\max} - T}{\Delta T}$	Logan-10	Logan <i>et al.</i> (1976)
$r(T) = e^{\rho T} - e^{\left(\rho T_{\max} - \frac{T_{\max} - T}{\Delta T} \right)}$	Logan-6/Lactin-1	Lactin <i>et al.</i> (1995)
$r(T) = e^{\rho T} - e^{\left(\rho T_{\max} - \frac{T_{\max} - T}{\Delta T} \right)} + \lambda$	Logan-6 /Lactin-2	Lactin <i>et al.</i> (1995)
$r(T) = aT(T - T_{\min})(T_{\max} - T)^{\frac{1}{2}}$	Analytis-3/Briere-1	Briere <i>et al.</i> (1999)
$r(T) = aT(T - T_{\min})(T_{\max} - T)^{\frac{1}{n}}$	Analytis-3/Briere-2	Briere <i>et al.</i> (1999)

T – the rearing temperature ($^{\circ}\text{C}$), ρ – a constant defining the rate at optimal temperature, T_{\max} – the lethal maximum temperature, ΔT – the temperature range over which physiological breakdown becomes the overriding influence and λ forces the curve to intercept the Y-axis at a value below zero, λ allows the curve to intersect the abscissa at suboptimal temperatures and, thus, allowing estimation of a lower developmental threshold, ψ , a , K and n are empirical constant parameters

Table 2. Developmental time of *S. maydis* at various constant temperatures

Developmental stage	Temperature [$^{\circ}\text{C}$]				
	15	20	25	30	32.5
1st instar	5.02 \pm 0.12 b	3.98 \pm 0.09 c	3.34 \pm 0.12 d	2.32 \pm 0.07 e	5.40 \pm 2.83 a
2nd instar	4.45 \pm 0.11 a	2.95 \pm 0.06 c	2.79 \pm 0.10 c	2.28 \pm 0.77 d	3.69 \pm 0.30 b
3rd instar	3.61 \pm 0.10 a	2.33 \pm 0.05 b	2.21 \pm 0.10 b	2.15 \pm 0.07 b	3.11 \pm 0.20 a
4th instar	3.38 \pm 0.15 a	1.86 \pm 0.08 b	1.83 \pm 0.15 b	1.68 \pm 0.12 b	–
Pre-imaginal time	17.28 \pm 0.33 a	12.15 \pm 0.17 b	10.85 \pm 0.26 c	9.55 \pm 0.26 d	–

Similar letters (a, b, c) in the rows indicate no significant differences ($p < 0.05$) at various constant temperatures by SNK test

Table 3. Linear regression of developmental rate $r(T)$ and temperature (T) for total immature developmental of *S. maydis*

Model	Regression equation	T_0	K	R^2_{adj}	R^2
Campbell <i>et al.</i>	$r(T) = 0.0030T - 0.0166$	-5.52	332.22	0.94	0.96

T_0 – lower developmental threshold; K – thermal constant; R^2 – coefficient of determination; R^2_{adj} – coefficient of non-linear regression

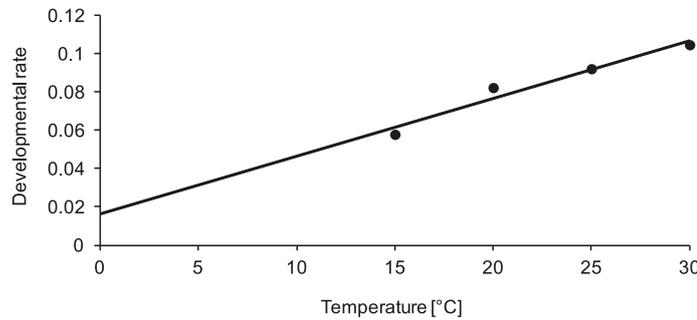


Fig. 1. Developmental rate for total immature developmental of *S. maydis* at different constant temperatures

In this research, T_0 and K of *S. maydis* were estimated -5.52°C and 332.22 degree-days, respectively (Table 3). The linear regression model of developmental rate and temperature for total immature development of *S. maydis* is presented in figure 1. According to the regression line slope, a positive relationship was observed between developmental rate and studied temperature range (15–30°C).

The estimated of the optimal temperature and higher temperature threshold of *S. maydis* by Analytis-3/Briere-1 model as non linear model was in agreement with observed data (Table 4). The six developmental rate non-linear models were compared based on the R^2 , R^2_{adj} and AIC (Table 4). The estimates of the optimal temperature for pre-imaginal development of *S. maydis* by the Logan-6, Logan-10, Logan-6/Lactin-1, Logan-6/Lactin-2, Analytis-3/Briere-1 and Analytis-3/Briere-2 models were 32.71, 34.04, 31.90, 35.53, 31.02 and 31.00°C, respectively. The lowest AIC were obtained by the Analytis-3/Briere-1 equation. This model had also high R^2 and R^2_{adj} and low RSS (Fig. 2).

Survival rate, life expectancy and entropy parameter

The l_x at age of adult emergence of *S. maydis* at 15, 20, 25, and 30°C were 0.58, 0.80, 0.76 and 0.46, respectively. The survivorship curves of the pest for different constant temperatures (Fig. 3A). The age specific survival at four temperatures decreased with increasing the aphid age. Survivorship of aphid decreased more rapidly to zero at 30°C. The e_x of one-day-old aphid were estimated to be 23.86, 36.54, 22.28 and 11.90 days at 15, 20, 25 and 30°C, respectively and life expectancies of adults at emergence were 21.40, 33.35, 19.24 and 14.76 days, respectively (Fig. 3B).

The values of entropy parameter of *S. maydis* (H) at 15, 20, 25 and 30°C were 0.65, 0.47, 0.43 and 0.80, respectively. These values indicated that the survival schedule of *S. maydis* was convex at 20 and 25°C ($H < 0.5$) and correspond to Deevey’s type I survivorship curves, but survivorship curves were type III at 15 and 30°C ($H > 0.5$).

Table 4. The values of the measurable parameters of Analytis-3/Briere-1 model for describing development time of each nymphal stages of *S. maydis*

Nymphal instar	Parameters						
	α	T_0	T_{max}	T_{opt}	R^2	R^2_{adj}	AIC
1st nymphal instar	0.00026	5.52	33.33	27.51	0.887	0.795	-61.534
2nd nymphal instar	0.00021	-0.81	34.09	27.50	0.923	0.872	-66.646
3rd nymphal instar	0.00020	-6.80	34.12	28.00	0.981	0.968	-73.764
4th nymphal instar	0.00025	-4.44	35.17	29.00	0.944	0.907	-63.449
Pre-imaginal development time	0.00003	-7.82	36.94	31.02	0.958	0.930	-68.805

α – the pre-imaginal development time; T_{opt} – the optimum temperature; T_0 – lower developmental threshold; T_{max} – the lethal maximum temperature; R^2 – coefficient of determination; R^2_{adj} – coefficient of non-linear regression; AIC – Akaike information criterion

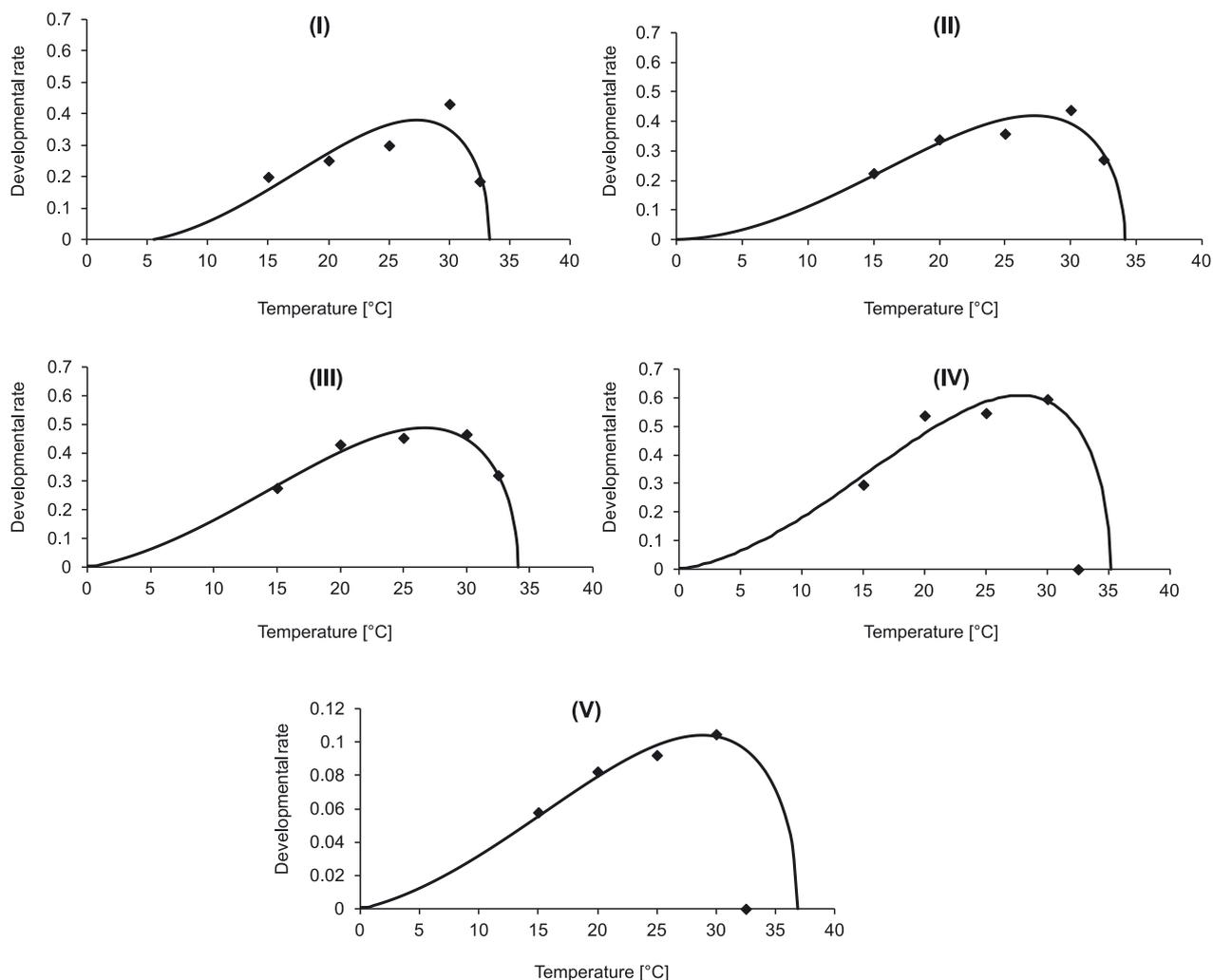


Fig. 2. Predicted rate of development of *S. maydis* as a function of temperature by Analytis-3/Briere-1 model for first (I), second (II), third (III), fourth (IV) nymphal instars and total developmental rate (V)

Adult longevity and fecundity

One-way ANOVA showed a significant difference among female adult longevity at different constant temperatures ($F = 15.85$, $df = 3, 122$, $p < 0.05$). The results showed that the mean longevity of females was the highest (33.59 days) at 20°C. Nevertheless, there was no significant difference among the mean adult longevity of *S. maydis* at 15, 25 and 30°C (Table 5). The pre-nymphopositional, nymphopositional,

and post-nymphopositional periods were affected significantly by temperature ($F = 7.20$, $df = 3, 122$, $p < 0.05$; $F = 16.88$, $df = 3, 122$, $p < 0.05$; and $F = 3.08$, $df = 3, 122$, $p < 0.05$, respectively) (Table 5). The highest nymphopositional period occurred at 20°C (30.62 days). Temperature had significant effect on mean fecundity per female ($F = 33.53$, $df = 3, 122$, $p < 0.05$) (Fig. 4). The mean fecundity at 15, 20, 25 and 30°C were 21.24 ± 1.97 , 44.82 ± 3.18 , 22.25 ± 2.33 and 16.39 ± 1.15 nymphs, respectively.

Table 5. Adult longevity and reproductive periods \pm SE for females of *S. maydis*

Parameters	Temperature [°C]			
	30	25	20	15
Pre-nymphopositional period	1.07 \pm 0.14 a	0.51 \pm 0.12 b	0.55 \pm 0.20 b	0.29 \pm 0.07 b
Nymphopositional period	17.72 \pm 1.91 b	30.62 \pm 2.30 a	17.45 \pm 1.06 b	15.76 \pm 0.98 b
Post-nymphopositional period	1.31 \pm 0.36 ab	2.46 \pm 0.53 a	0.60 \pm 0.26 b	2.32 \pm 0.45 a
Adult longevity	20.1 \pm 2.08 b	33.59 \pm 2.47 a	18.60 \pm 0.21 b	18.37 \pm 1.12 b
Life span	37.72 \pm 2.02 b	45.74 \pm 2.45 a	29.45 \pm 1.16 c	27.92 \pm 1.08 c

Similar letters (a, b, c) in the rows indicate no significant differences ($p < 0.05$) at various constant temperatures by SNK test. Pre-nymphopositional period is defined as the number of days from adult satage of an aphid to the birth of its first offspring. Nymphopositional period is defined as the number of days from the first to last birth per mother aphid. Post-nymphopositional period is defined as the number of days from last birth of an aphid per mother aphid to death of mother aphid

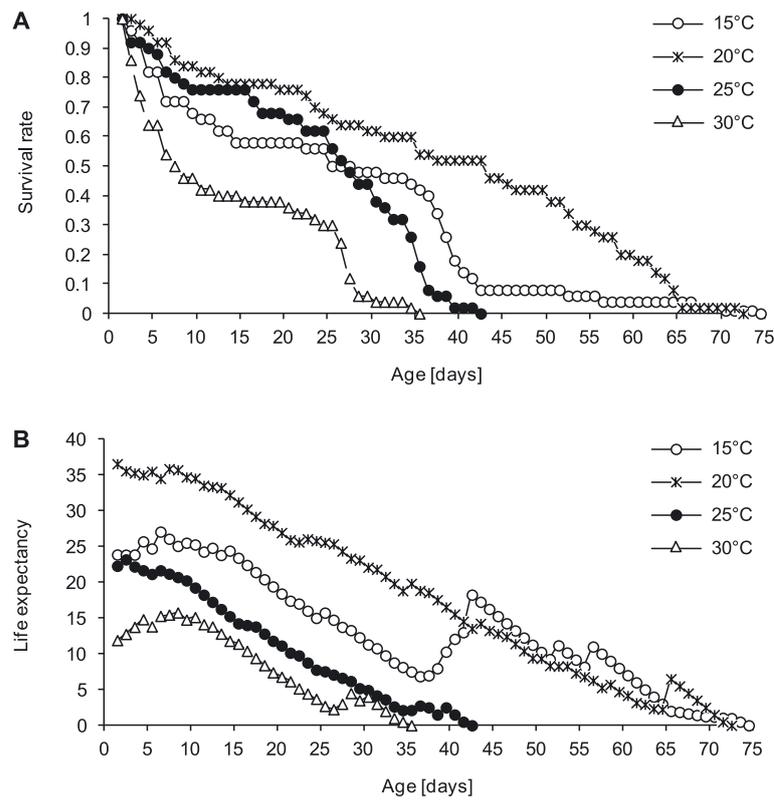


Fig. 3. Age-specific survival rate (l_x) (A) and life expectancy (e_x) (B) of *S. maydis* at different constant temperatures

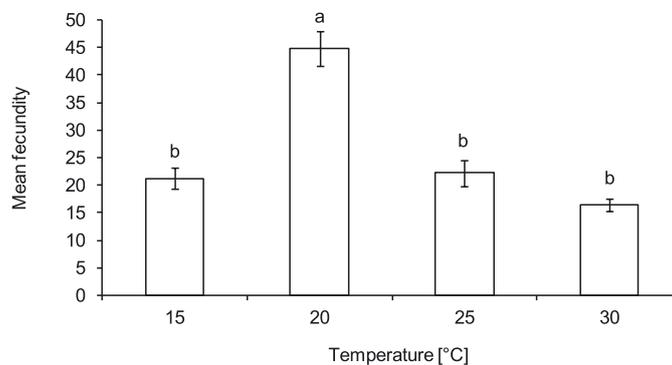


Fig. 4. Mean fecundity (nymphs/female/generation) of *S. maydis* at different constant temperatures

Demographic parameters and growth index

The values of demographic parameters and growth index of *S. maydis* at each of the four temperatures studied are listed in table 6. The R_0 , r_m , λ , T and DT were influenced significantly by the temperatures (R_0 : $F = 48.55$, $df = 3, 120$, $p < 0.05$; r_m : $F = 12.32$, $df = 3, 120$, $p < 0.05$; λ : $F = 11.53$, $df = 3, 120$, $p < 0.05$; T : $F = 26.94$, $df = 3, 120$, $p < 0.05$; DT : $F = 27.42$, $df = 3, 120$, $p < 0.05$). The net reproductive rate was highest at 20°C, with 35.04 nymphs per female per generation time. As temperature increased, the r_m followed a typical asymmetrical dome-shape pattern, with maximum value of 0.173 ± 0.012 females/female/day at 20°C. The highest and lowest values of finite rate of increase were observed at 20 and 15°C, respectively. The T decreased with increasing temperature. The cohort reared at 20 and 25°C had the lowest value DT (3.99 ± 0.26

and 4.47 ± 0.099 days, respectively). The growth index at 20°C was about twice as high as at 15°C, and substantially higher than other temperatures (25 and 30°C).

Discussion

Although insects live in a variable environment with temperature fluctuations, therefore study on the effect of temperature can be very useful in understanding the population dynamics of various insects (Summers *et al.* 1984; Kontodimas *et al.* 2004; Stathas *et al.* 2011). The results of this research proved that temperature has significant effect on the demographic parameters and biological characteristics of *S. maydis*. The demographic parameters provide population growth rates of an insect (Frei *et al.* 2003), and therefore understanding them is essential to develop an integrated pest management strategy.

Table 6. Effect of temperatures on demographic parameters (\pm SE) and growth index of *S. maydis*

Parameters	Unit	Temperature [°C]			
		15	20	25	30
R_0	females/female/generation time	12.52 \pm 1.14 b	35.04 \pm 2.48 a	13.24 \pm 1.08 b	8.9 \pm 0.892 b
r_m	females/female/day	0.109 \pm 0.003 c	0.173 \pm 0.012 a	0.155 \pm 0.003 ab	0.143 \pm 0.007 b
λ	day ⁻¹	1.12 \pm 0.003 c	1.19 \pm 0.014 a	1.17 \pm 0.004 ab	1.15 \pm 0.008 b
T	day	23.21 \pm 0.805 a	21.95 \pm 0.689 a	16.32 \pm 0.357 b	14.88 \pm 1.15 b
DT	day	6.35 \pm 0.160 a	3.99 \pm 0.26 c	4.47 \pm 0.099 bc	4.84 \pm 0.239 b
GI	–	0.033	0.069	0.062	0.038

R_0 – net reproductive rate; r_m – intrinsic rate of natural increase; λ – finite rate of increase; T – mean generation time; DT – doubling time; GI – growth index

Similar letters (a, b, c) in the rows indicate no significant differences ($p < 0.05$) at various constant temperatures by SNK test

S. maydis was successfully developed from 15 to 30°C. The aphids failed to completed development at 32.5°C. The T_0 was -5.52°C for *S. maydis*. The result of this research was also showed that *S. maydis* required 332.22 DD. Tazerouni *et al.* (2013) reported that T_0 and K of *D. noxia* were 3.6°C and 147.1 DD, respectively. While *Schisaphis graminum* (Rondani) need 133.33 degree-days for development from birth to adult and its T_0 was reported 5.73°C (Tofangsazi *et al.* 2010). The T_0 and K values of *D. noxia* on wheat were estimated -1.6°C and 225.57 DD (Girma *et al.* 1990) by linear Campbell model. Our finding showed that *S. maydis* is a cold resistance species in comparison to other cereal aphids. These differences could be attributed to differences in species and/or temperature treatments. Temperature is known to differentially affect the development of aphids (Campbell *et al.* 1974). The Analytis-3/Briere-1 model was accepted for success to satisfy criteria of goodness-of-fit and estimable temperature threshold parameters and highly recommended for the description of temperature-dependent development of *S. maydis*. The Lactin 2 model was exhibit high efficiency in modeling the development rate of rice root aphid, *Rhopalosiphum rufiabdominalis* (Sasaki) (Tsai and Liu 1998). Ma and Bechinski (2008) reported that Stinner model was the best fit to the developmental rate of *D. noxia* on barley. The Analytis-3 developmental model was recommended for description of temperature dependent development of *Sitobion avenae* (F.) (Farhad *et al.* 2012). The Analytis-3/Briere-1 model was also introduced as one of the best models for the description of temperature-dependent development of *D. noxia* (Tazerouni *et al.* 2013).

The entropy value is a summary of the degree of concavity of survival schedule. If $H = 0$, then all deaths occur at exactly the same age and the shape of the l_x schedule is rectangular. If all individuals have exactly the same probability of dying at each age, the shape of the survival schedule exponentially decreases and $H = 1$ (Carey 2001). In this research, the values of this parameter for *S. maydis* was lower than 0.5 at 20 and 25°C. Therefore the survival schedule of this aphid was convex at these temperatures. These evidently suggest that the death probability was high in later ages compared with early ones. But values of entropy of *S. maydis* were higher than 0.5 at 15 and 30°C, these show that the death probability was high in early ages. Furthermore, entropy parameter as quantita-

tive characterization of survival patterns showed that the magnitude of the effects of changes in mortality rates on life expectancy differed substantially among temperatures.

Low (15°C) and high temperatures ($> 20^\circ\text{C}$) had a marked negative effect on adult longevity of *S. maydis* (Table 2). The similar results were observed in nymphositional period of *S. maydis*. The highest pre-nymphositional period obtained at 15°C. The mean total number of nymphs per female was highest at 20°C (44.82 \pm 3.18) and lowest at 30°C (16.38 \pm 1.15). The average total nymphs produced by a female of *D. noxia* and *S. graminum* were ranged from 49.71 \pm 1.44 to 2.91 \pm 0.26 nymphs and from 66.14 \pm 3.47 to 16.38 \pm 0.60 nymphs, respectively at fluctuating temperatures that averaged from 10 to 30°C (Tofangsazi *et al.* 2010; Tazerouni *et al.* 2013).

Demographic parameters of *S. maydis* varied noticeably depending upon temperature. In the present study, the R_0 at 20°C was much higher than those obtained on the other temperatures. The high value of R_0 at 20°C resulted from low mortality of the immature life stages and also of adults between emergence and peak nymphosition and is reflected in high r_m value. The r_m of *S. maydis* estimated in the current study ranged from 0.173 \pm 0.012 and 0.109 \pm 0.003 females/female/day. The highest intrinsic rate of natural increase of *S. maydis* occurred at 20°C. Several factors such as fecundity, survival and specifically generation time affect r_m and this parameter adequately summarizes the physiological qualities of an insect in relation to its capacity to increase, so it would be a most appropriate index to evaluate the performance of an insect at different temperatures (Kocourek *et al.* 1994; Southwood and Henderson 2000), different host plants (Goławska 2010) and host plant quality (Rostami *et al.* 2012). The highest value of finite rate of increase was obtained in population reared at 20°C (1.19 \pm 0.014 days). The doubling time was 3.99 \pm 0.26 at 20°C and its value was significantly shorter than the other temperatures. The growth index (Ramasubramanian and Babu 1989) for insects reared at 15 and 30°C was lower than that observed for *S. maydis* reared at 20 and 25°C. Ricci and Kahan (2005) studied the demographic parameters of *S. maydis* on barley at 20°C and demographic parameters including R_0 , r_m , T and DT values reported 74.76 \pm 1.888 females/female/generation, 0.198 \pm 0.002 females/female/day, 28.364 days and 3.50

days, respectively. The different results of various studies could be attributed to differences of experimental conditions as well as to strains of *S. maydis*.

According to the whole estimated population growth parameters, the optimum temperature for the *S. maydis* outbreaking seems to be 20°C. The population growth parameters may be affected by geographical region, host plants, and experimental conditions. Accordingly our findings provide fundamental information and when this information is used in association with other ecological data, it may be valuable in development and implementation of management programs of *S. maydis* in wheat fields.

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