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Temperature Dependent Life History Traits of *Brevicoryne brassicae* (L.) (Hom., Aphididae) on White Cabbage

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Abstract: The developmental time, survival rate and reproduction of the cabbage aphid, *Brevicoryne brassicae* (L.) (Homoptera, Aphididae), were evaluated on detached cabbage leaves (*Brassicae oleracea* var. *capitata*) at four constant and two alternating temperatures (15, 20, 25, 30, 25/30 and 30/35 °C). Developmental periods of immature stages ranged from 12.5 days at 15 °C to 6.0 days at 25/30 °C. The alternating temperature of 30/35 °C was lethal to immature stages of *B. brassicae*. The lower developmental threshold for the cabbage aphid was estimated at 4.0 °C and it required 142.9 degree-days for a first instar to become an adult. The average longevity of adult females was reduced from 16.3 days at 15 °C to 9.8 days at 30 °C. The average reproduction rate per female (R_0) was 47.1 aphids/aphid at 25 °C and 1.5 aphids/aphid at 30 °C. Mean generation time (T_0) of the population ranged from 11.3 days at 30 °C to 22.6 days at 15 °C. The highest per capita growth rate (r_m = 0.317 aphids/aphid per day) occurred at 25 °C, and the lowest at 30 °C (r_m = 0.037 aphids/aphid per day). It was evident that temperatures above 25/30 °C prolonged development, increased the mortality of immature stages, shortened adult longevity and reduced fecundity. The optimal range of temperature for the population growth of *B. brassicae* on white cabbage was 20 to 25/30 °C.

Key Words: *Brevicoryne brassicae*, development, longevity, fecundity, intrinsic rate of increase, white cabbage

Brevicoryne brassicae (L.) (Hom., Aphididae)'nin Lahana Üzerinde Sıcaklığa Bağlı Yaşam Tablosu Değerleri

Özet: Lahana unlu yaprakbiti, *Brevicoryne brassicae* (L.) (Homoptera, Aphididae)'nin gelişme süresi, yaşam oranı ve üreme kapasitesi kesilmiş lahana yaprakları (*Brassicae oleracea* var. *capitata*) üzerinde dört sabit ve iki değişken sıcaklıkta (15, 20, 25, 30, 25/30 ve 30/35 °C) araştırılmıştır. Ergin öncesi toplam gelişme süreleri 15 °C'de 12.5 gün ile 25/30 °C'de 6.0 gün arasında gerçekleşmiştir. Değişken sıcaklıklardan 30/35 °C *B. brassicae*'nin ergin öncesi dönemleri için öldürücü olmuştur. Lahana unlu yaprakbiti'nin gelişme eşiği 4.0 °C hesaplanırken, birinci dönem nimfin ergin olması için gerekli olan sıcaklıklar toplamı ise 142.9 gün-derece olarak tespit edilmiştir. Ergin dişilerin ömür uzunlukları 15 °C'de 16.3 gün iken bu süre azalarak 30 °C'de 9.8 güne düşmüştür. Dişi başına ortalama net üreme gücü (R_0) 25 °C'de 47.1 afit/afit iken 30 °C'de 1.5 afit/afit hesaplanmıştır. Populasyonun ortalama döl süresi (T_0) 11.3 gün (30 °C) ile 22.6 gün (15 °C) arasında bulunmuştur. En yüksek kalıtsal üreme yeteneği 25 °C (r_m = 0.317 afid/afid/gün)'de hesaplanırken, en düşük ise 30 °C (r_m = 0.037 afid/afid/gün)'de hesaplanmıştır. Elde edilen bulgular 25/30 °C'nin üstündeki sıcaklıklarda Lahana unlu yaprakbitinin daha uzun bir gelişme süresi göstermiş ve bununla birlikte ergin öncesi dönemlerde de yüksek ölüm oranı, ömür uzunluğunun kısalması ve üreme gücünün azaldığı saptanmıştır. *B. brassicae*'nin lahana üzerindeki populasyon gelişmesi için en uygun sıcaklık aralığı 20 - 25/30 °C'dir.

Anahtar Sözcükler: *Brevicoryne brassicae*, gelişme süresi, ömür uzunluğu, üreme gücü, kalıtsal üreme yeteneği, lahana

Introduction

The cabbage aphid, *Brevicoryne brassicae* (L.) (Homoptera, Aphididae), a pest on many cruciferous crops is distributed throughout all the temperate and warm temperate regions of the world. This aphid is considered one of the most damaging and consistently present pests on cabbage crops (Theunissen, 1989). *B. brassicae* causes direct damage, resulting from searching

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for food, which may induce plant deformation (Ibbotson, 1953; Oatman and Platner, 1969), and indirect damage caused either by honeydew or by transmission of viruses. The cabbage aphid is a vector of 20 virus diseases in a large range of plants (Chan et al., 1991).

Several studies have shown that the morphology and temperature dependent development of aphids including *B. brassicae* may be strongly influenced by the geographical origin of the aphid (Campbell et al., 1974; Foottit and Mackauer, 1990; Mokhtar et al., 1993), while other authors emphasize the effect of host plants on morphological variations and aphid development (Wool and Hales, 1996; 1997; Kersting et al., 1998; Van Lerberghe-Masutti and Chavigny, 1998; Satar et al., 1999). Thus, developmental and fecundity data for *B. brassicae* on one host plant and from one region should be used with caution if applied to different crops and regions.

The present study was designed to provide data on the developmental rate and fecundity of a Turkish population of *B. brassicae* at different constant and alternating temperatures that might be used for developing integrated pest management strategies, in particular monitoring and sampling plant of the cabbage aphid in the East Mediterranean region of Turkey.

Materials and Methods

Experimental design. *B. brassicae* individuals were obtained from white cabbage (*Brassicae oleracea var. capitata*) near Adana in the East Mediterranean region of Turkey and maintained on white cabbage leaf disks (cv. "Yalova 1"), placed upside down on wet cotton in Petri dishes (Ø 5 cm) at 25 ± 1 ºC and 65 ± 10% relative humidity, and given 16 h of artificial light of about 5,000 Lux, in a temperature cabinet. The cotton in the Petri dishes was daily saturated with water and the leaf disks were changed every three days. Aphids had been reared in the laboratory for 2-3 generations before individuals were used in the experiments (Kindlmann and Dixon, 1989).

Randomly selected apterous females from the stock culture were transferred onto excised cabbage leaf disks placed upside down in Petri dishes. Offspring born within 24 h were confined individually on cabbage leaf disks in Petri dishes. All replications in which nymphs died within 24 h after transfer or were lost during the experiment were omitted. The cotton in the Petri dishes was wetted daily, and aphids were transferred to new cabbage leaf disks every 3-5 days. Leaves used in the experiments were obtained from field-grown white cabbage near Adana, Turkey, between 6 to 12 weeks of age.

Experiments were conducted at four constant temperatures ranging from 15 to 30 ± 1 ºC in 5 ºC increments and at two alternating temperatures of 25/30 ± 1ºC and 30/35 ± 1 ºC with an abrupt transition after 12 h, 60 ± 5 %r. h. and 16 h of artificial light (5000 Lux) in temperature cabinets. Immature stages and adults were observed daily at all temperature regimes and their survivorship recorded. The exuviae were used to determine molting time. Newly born nymphs were removed after counting.

Data analysis. Differences in developmental time, longevity and reproduction were tested using ANOVA. If significant differences were detected, multiple comparisons were made using Tukey's HSD MRT (P = 5%). A linear technique was employed to compute the lower development threshold of the nymph stages by using growth rate data as dependent variables and temperature treatments as independent variables. The means of the alternating temperatures (27.5 ºC for 25/30 ºC and 32.5 ºC for 30/35 ºC) were used in the regression analysis. 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.

Population growth rates were calculated from Lotka equation (Birch, 1948):

$$1 = \Sigma\, e^{-r*x}\, l_x * m_x \qquad (1)$$

in which x = age in days (including immature stages), r = intrinsic rate of increase, l_x = age specific survival (including immature mortality), and m_x = age specific number of female offspring.

After r was computed for the original data (r_{all}), differences in r_m-values were tested for significance by estimating variances using the jackknife method (Meyer et al., 1986). The jackknife pseudo-value r_j was calculated for the n samples using the following equation:

$$r_j = n * r_{all} - (n-1) * r_i \qquad (2)$$

The mean of (n-1) jackknife pseudo-values for each treatment was subjected to analysis of variance. Tukey's HSD MRT was used to compare mean growth rates at different temperatures (P = 1%). Because low probability levels were used, there was no concern over inflation of experiment-wise error rates (Jones, 1984). Each of the above mentioned analyses was conducted using the Statgraphics software package (Statistical Graphics Corporation, 1988).

Results

The cabbage aphid showed significantly decreased developmental times with an increase in temperature, ranging from 12.5 days at 15 ºC to 6.0 days at 25/30 ºC (F = 168.4; df = 4, P < 0.1%) (Table 1). The alternating temperature of 30/35 ºC was lethal to early nymphal stages of *B. brassicae*. High mortality rates also occurred at 15 ºC (26.7%), and at 25/30 and 30 ºC, at 33.3% and 42.9%, respectively.

A linear regression analysis was applied to the developmental points within the 15 – 25/30 ºC range. Development at 30 ºC was outside the linear segment of the growth curve and was therefore excluded from the linear regression. Within the chosen temperature range, the developmental rates ($r_{(T)}$) of the cabbage aphid increased linearly with increasing temperature ($r_{(T)} = 0.007 * T - 0.0279$; $R^2 = 0.990$; F = 198.4; P < 1%) (Figure 1). The theoretical developmental threshold was estimated at 4.0 ºC. It required 142.9 degree-days for a first instar to become an adult based on the development threshold for overall immature stages.

Longevity varied only slightly between 15 and 25/30 ºC ranging from 16.3 to 14.2 days. *B. brassicae* had the shortest longevity at 30 ºC at only 9.8 days (F = 2.66; df = 4; P < 5%). The highest mean fecundity per reproduction day occurred between 20 and 25/30 ºC with 3.5 to 4.2 nymphs per female and day. Significantly fewer nymphs per day were deposited at 15 and 30 ºC (F = 12.48; df = 4; P < 0.1%) (Table 1).

Table 1. Developmental time, longevity, mortality and fecundity rate of *Brevicoryne brassicae* on excised white cabbage leaf disks at six temperature regimes.

Temperature (ºC)	n	Developmental time (days) (mean ± SEM)	Total nymphal mortality rate (%)	Longevity (days) (mean ± SEM)	Offspring per reproduction day (mean ± SEM)
15 ± 1	33	12.5 ± 0.26 d	26.7	16.3 ± 1.54 a	2.4 ± 0.42 ab
20 ± 1	29	9.3 ± 0.20 c	5.3	14.5 ± 0.79 ab	3.5 ± 0.18 bc
25 ± 1	37	6.9 ± 0.15 b	11.9	15.6 ± 1.10 b	4.2 ± 0.18 c
30 ± 1	24	7.3 ± 1.29 b	42.9	9.8 ± 1.01 a	1.3 ± 0.24 a
25 / 30 ± 1	28	6.0 ± 0.70 a	33.3	14.2 ± 1.04 ab	3.9 ± 0.26 c
30 / 35 ± 1	46	-	100.0		

Means in columns followed by the same letter are not significantly different by Tukey's HSD MRT (P = 5%)

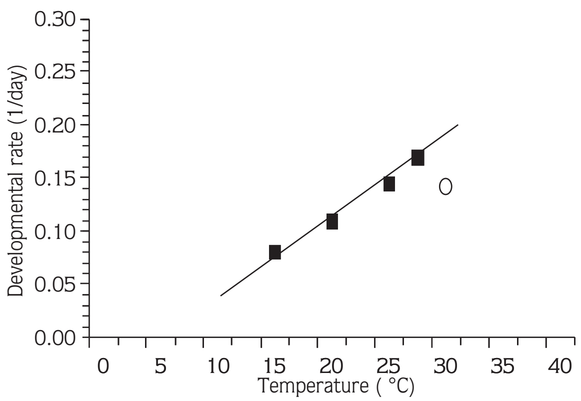

Figure 1. Developmental rate of *Brevicoryne brassicae* at three constant (black circles) and one alternating temperature (open circle) on excised white cabbage leaf disks. The line is the linear regression analysis of developmental rate and temperature within the range 15 to 25/30 ºC. The mean of the alternating temperatures (27.5 ºC for 25/30 ºC) was used for the regression analysis.

Adults of *B. brassicae* had almost no post-reproductive period at all temperatures tested, with relatively long survival rates at 15 – 25/30 ºC (Figure 2). The highest age-specific number of nymphs per female per day (m_x) ranged between 0.16 at 30 ºC and 6.83 at 25 ºC. Increasing temperatures resulted in shorter generation times (T_0) of the cabbage aphid, at 22.6 days at 15 ºC and 11.3 days at 30 ºC (Table 2). The net reproductive rate (R_0) was highest at 25 ºC (47.1 aphids/aphid) and lowest at 30 ºC with less than 1.5 aphids/aphid (Table 2). *B. brassicae* kept at a warm temperature of a constant 30 ºC had significantly lower per capita rates of population growth with only 0.037 aphids/aphid per day, followed by those kept at 15 ºC with 0.144 aphids/aphid per day ($F = 37.43$; $df = 4$; $P < 0.1\%$). The intrinsic rate of increase did not significantly differ for the cabbage aphid between 20 and 25/30 ºC, ranging on a high level between 0.249 and 0.317 aphids/aphid per day.

Discussion

Temperature has the major effect on the biology and life cycle of aphids. Controlled laboratory studies can provide detailed information about the population dynamics of aphids. Our results clearly show the effects of temperature on the developmental time, nymphal mortality rate, longevity and fecundity of *B. brassicae* on excised leaf disks of white cabbage.

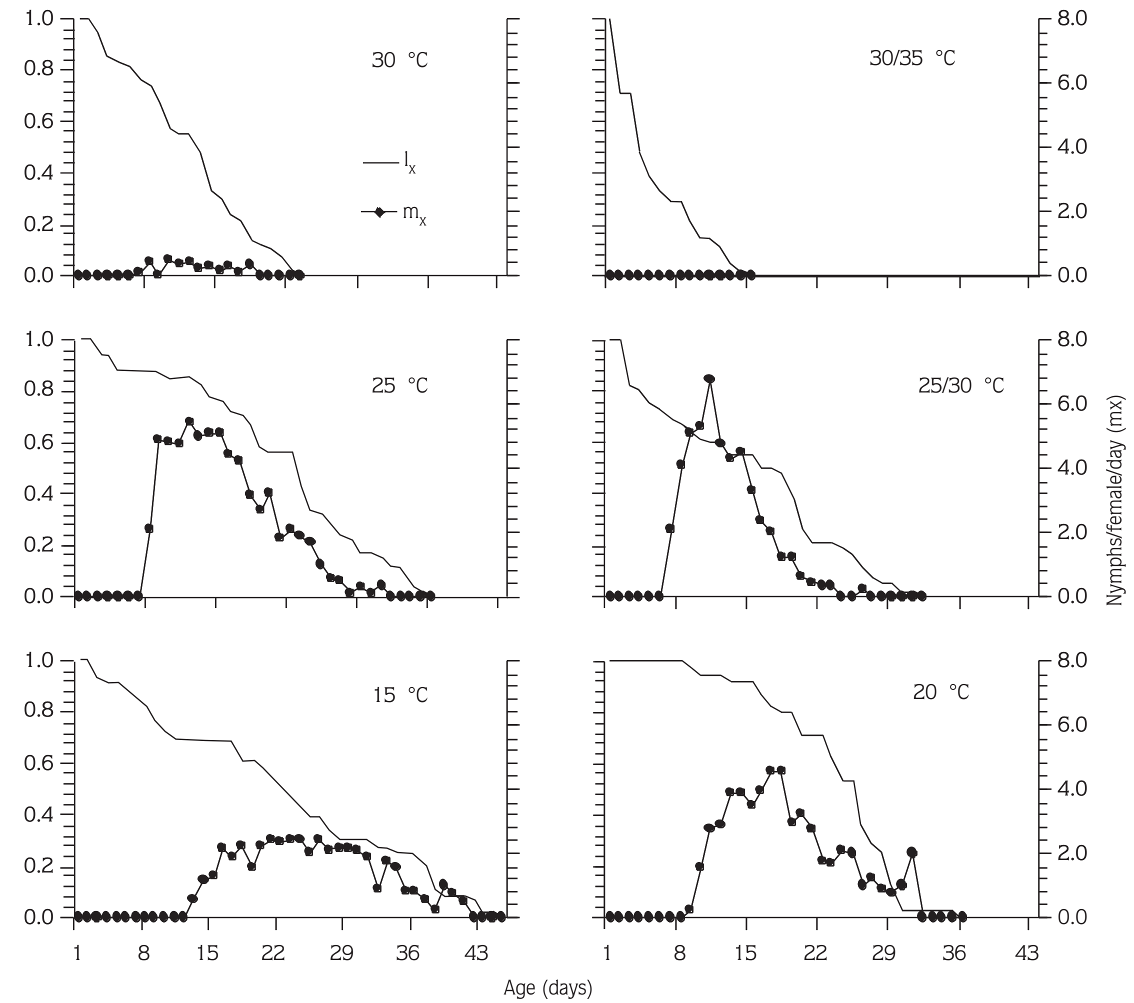

Figure 2. Age-specific survival rate (l_x) and age-specific fecundity (m_x) of *Brevicoryne brassicae* on excised white cabbage leaf disks at 6 temperature regimes.

Table 2. Generation time (T_o), net reproductive rate (R_o) and rate of population growth (r_m) of *Brevicoryne brassicae* on excised white cabbage leaf disks at five temperature regimes.

Temperature (ºC)	Generation time (T_o) (days)	Reproduction rate (R_o) (aphids/aphid)	Intrinsic rate of increase (r_m) (aphids/aphid/day)
15 ± 1	22.6	20.3	0.144 ± 0.0068 a
20 ± 1	16.7	40.5	0.249 ± 0.0076 b
25 ± 1	14.2	47.1	0.317 ± 0.0088 b
30 ± 1	11.3	1.5	0.037 ± 0.0376 c
25 / 30 ± 1	11.8	27.9	0.301 ± 0.0155 b

Means in column followed by the same letter are not significantly different by Tukey's HSD MRT (P = 1%)

Optimum temperature for the development of the cabbage aphid was 25/30ºC, and thus, similar to the result obtained by DeLoach (1974), who reported the shortest development period at 25 ºC. Insects reared at temperatures above the upper threshold develop slower than those reared under more favorable conditions (Stinner et al., 1974; Curry et al., 1978). This was also true for *B. brassicae* at 30 ºC, resulting in a significant increase in developmental time compared to 25/30 ºC. The theoretical lower development threshold of 4.0 ºC, computed from the linear segment of the growth curve, was similar to the 3-4 ºC reported from Israel (Elze, 1944; Bonnemaison, 1951) and the 4.7 ºC reported by Campbell et al. (1974) for a Vancouver population of *B. brassicae*. In contrast, a considerably lower developmental threshold (1.7 ºC) for the cabbage aphid was obtained from Finland by Markkula (1953). These results are in agreement with those of Campbell et al. (1974), who stated that the development threshold of aphids originating from warm summer or mild spring climates should be higher than those from cooler climates. The East Mediterranean region of Turkey, with its typical Mediterranean climate with warm summers and cool humid winters, resulted in a slightly higher development threshold for the cabbage aphid than those obtained in the slightly warmer climate of Israel. Significantly lower values were observed for the cold climate in Finland.

The intrinsic rate of natural increase (r_m) is a good indicator of the temperature at which the growth of a population is most favorable, because it reflects the overall effects of temperature on development, reproduction and survival characteristics of a population. *B. brassicae* kept at 25 ºC had the highest r_m-value among all temperatures (r_m = 0.317 aphids/aphid per day), because of the faster development and higher survivorship of immature stages as well as the high daily rate of progeny. However, the capita growth rate at 25 ºC was not statistically different from those at 20 ºC and 25/30 ºC. In contrast, the population exposed to 15 ºC had a prolonged developmental time and a higher immature stage mortality rate, resulting in a much smaller intrinsic rate of increase (0.144 aphids/aphid per day). The capita growth rate of the *B. brassicae* used in our studies was considerably higher for all temperatures tested than those reported by DeLoach (1974). These differences were due to a much longer generation time and considerably lower reproduction rates. Closer to our own results, Hoseini et al. (2003) reported an r_m-value of 0.25 aphids per aphid/day at 25 ºC, and Ölmez Bayhan (2004) reported 0.2009 aphids/aphid per day at 20 ºC.

According to our results, *B. brassicae* populations in the East Mediterranean region of Turkey are well adapted to temperatures between 20 and 27.5 ºC, showing a high capita growth rate within this temperature range. Temperatures below or above this range result in drastically reduced population growth, and temperatures over 30 ºC are lethal to nymphs of the cabbage aphid. With this information it should be now possible to establish monitoring and sampling plans for this important cabbage pest as a first step in developing IPM programs.

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