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Plant Resistance

Population Growth of *Dysaphis pyri* (Hemiptera: Aphididae) on Different Pear Cultivars With Discussion on Curve Fitting in Life Table Studies

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Abstract

Population growth parameters of the *Dysaphis pyri* (Boyer de Fonscolombe) (Hemiptera: Aphididae) were evaluated on four different cultivars (Coscia, Ankara, Williams, and Santa-Maria) of pear (*Pyrus communis* L.) under field conditions in the Van region of Turkey. Aphids were kept on leaves of 10-yr-old pear trees in Plexiglas clip-cells (20 mm in diameter and 10 mm in height, with the upper side covered with muslin). For the description of the stage differentiation during population growth, we analyzed raw data of developmental time, survival, and fecundity using the age-stage, two-sex life table to take the variable developmental rate among individuals into account. Results indicated that the Coscia and Ankara cultivars are less favorable hosts for *D. pyri* because of the longer preadult developmental time, higher preadult mortality rate, and lower total fecundity on these cultivars. The intrinsic rate of increase (r), the net reproduction rate (R_0), and the finite rate of increase (λ) values were lower on the Coscia and Ankara cultivars. We discussed the application of the Weibull function, polynomial model, and Enkegaard model in life table studies. Because these models are often inaccurate in describing survival and reproduction parameters, we suggest that their application in life table research should be reevaluated.

Key words: *Dysaphis pyri*, pear, life table

The *Dysaphis pyri* (Boyer de Fonscolombe) (Hemiptera: Aphididae) is an important pest of the pear ecosystems in Turkey, which is a primary pear-producing country (Anonymous 2012). The aphid occurs in Europe, North Africa, South-West and Central Asia, including Nepal, Northern India, and Pakistan, and has been introduced into the United States (Blackman and Eastop 2000). As an heteroecious and holocyclic pest, its first two to three spring and early summer generations cause severe damage to pears before migrating to their summer hosts (*Galium* spp.; Blackman and Eastop 2000). Leaves and shoots of pear trees are yellowed and distorted to form pseudo-galls. Aphids produce considerable quantities of honeydew, further affecting growth. In addition, the curled leaves attract the pear psylla (*Cacopsylla pyri*) (Anonymous 2016). In Turkey, this aphid is quite common in early summer on the young shoots of local and standard cultivars of pear. Pesticide applications are required to suppress the aphid population in pear orchards in early summer.

The use of pesticides, however, not only disrupts natural biological control and decreases their potential effectiveness but also causes an increase in production costs. Since host plants can often affect the development, survival, and fecundity of insect herbivores (Painter 1951, Garad et al. 1984, Awmack and Leather 2002, Lee 2007) with their physical, chemical, or biological traits (e.g., size and structure, nutritional value, secondary compounds, and phenology), using resistant or less favorable plants is considered to be a major component of pest management programs. Plant susceptibility to phytophagous insects can be assessed by their behavioral responses (host finding, acceptance, and consumption rate), developmental responses (efficiency of food utilization, developmental rate, and survivorship), or combination of these processes (Phelan et al. 1995). The population growth rate of a pest species on a given host plant depends on its developmental responses. These are effectively measured by using life table data because life table parameters

reflect the combined effects of survival, development, fecundity, etc. on the growth of a population. Hence, the life table is an essential tool for assessing the overall performance of an insect pest on its host.

No information is currently available on the effects of pear cultivars on the population growth of *D. pyri*. In this study, life table data (i.e., development, survival, and fecundity) of the *D. pyri* were collected on four of the most commonly grown pear cultivars in Turkey. Although these aphid populations are parthenogenetic, in order to obtain precise description on the stage differentiation, life history raw data were analyzed based on the age-stage, two-sex life table (Atlihan and Chi 2008, Huang and Chi 2012, Polat-Akköprü et al. 2015). The information obtained from this study will be useful in future pest management programs developed for pear-producing agroecosystems.

Materials and Methods

The four cultivars of pear (*Pyrus communis* L.) used for the experiments were Coscia, Ankara, Williams, and Santa-Maria. *Dysaphis pyri* adults were collected from pear trees growing in the experimental orchard of the Faculty of Agriculture, University of Yuzuncu Yil in Van, Turkey. Aphids were reared on each pear cultivar for a generation to eliminate any possible effects from the previous hosts. Experiments were conducted using leaves from 10-yr-old pear trees grown in the same experimental orchard. A single adult aphid was transferred onto each leaf and covered by a Plexiglas clip-cell (20 by 10 mm) with the top and sides covered by muslin. All adult aphids and newborn nymphs, except one nymph, were removed from the cells after 24 h. Nymphal development and survival were observed at daily intervals, with the presence of an exuvium used as evidence for molting to the next developmental stage. After the emergence of adults, the reproductive period, longevity, survival, and reproduction of individuals were observed daily until the death of all individuals. During the reproductive period, newborn nymphs were recorded and then removed from the cells. All treatments were conducted during the same time period (June and July, 2010). During the experimental period, the average temperature was 20.6 C (ranging from 18.9. to 23.1 C), average RH was 45.6% (ranging from 42.7 to 48.6%), and photoperiod was 14:10 (L:D) h.

Data Analysis

Developmental time, survival, and fecundity data were analyzed based on the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988) to take into account the variable developmental rate that occurs in individuals (Chi and Liu 1985, Chi 1988). Raw data were used to calculate the age-stage-specific survival rate (s_{xj}, where x = age in days and j = stage), age-stage-specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), age-stage life expectancy (e_{xj}), age-stage reproductive value (v_{xj}), and life table parameters (R_0, net reproductive rate; r, intrinsic rate of increase; λ, finite rate of increase; and T, the mean generation). In the age-stage, two-sex life table, the l_x, m_x, and R_0 values are calculated as

$$l_x = \sum_{j=1}^{k} s_{xj} \tag{1}$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \tag{2}$$

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

where k is the number of stages. The intrinsic rate of increase was estimated using the iterative bisection method from the Euler-Lotka formula with age indexed from 0 (Goodman 1982):

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

The finite rate is calculated as $\lambda = e^r$. The mean generation time is defined as the length of time that a population needs to increase to R_0-fold of its population size at the stable age-stage distribution, and is calculated as $T = (\ln R_0)/r$. The life expectancy (e_{xj}) is the length of time that an individual of age x and stage j is expected to live and it is calculated according to Chi and Su (2006) as

$$e_{xj} = \sum_{i=x}^{\infty} \sum_{y=j}^{k} s'_{iy} \tag{5}$$

Where s'_{iy} is the probability that individuals of age x and stage j will survive to age i and stage y and, is calculated by assuming $s'_{xj} = 1$. The reproductive value (v_{xj}) was calculated according to Tuan et al. (2014a, b) and was calculated as

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}} \sum_{i=x}^{\infty} e^{-r(i+1)} \sum_{y=j}^{k} s'_{iy} f_{iy} \tag{6}$$

The computer program, TWOSEX-MSChart, was used in this analysis (Chi 2016). The program was written in Visual BASIC for the Windows operating system and is available at http://140.120.197.173/Ecology/Download/Twosex-MSChart.rar. Since simplified method can cause problems as pointed out by Carter et al. (1978) and Hesterberg (2008), we used the bootstrap technique (Efron and Tibshirani 1993, Huang and Chi 2012) with 200,000 resampling to estimate the variances and standard error of the population parameters. We used the paired bootstrap method to compare the different treatments. The bootstrap method is embedded in the computer program TWOSEX-MSChart.

Fitting Survival Rate (l_x) and Fecundity (m_x) to Models

The age-specific survival rate (l_x) was fitted to the cumulative 2-parameter Weibull distribution (Johnson et al. 1970, Pinder et al. 1978) using the formula

$$s_x = \exp\left[-\left(\frac{x}{b}\right)^c\right] \tag{7}$$

where S_x is the expected survival rate to age x, while b and c are two parameters that decide the scale and shape, respectively. To ensure a proper fit, we used both the nonlinear regression in Mathematica 8.0 (Wolfram Research 2011) and Weibull distribution in SigmaPlot to estimate the parameters b and c.

Enkegaard (1993) introduced following model to fit the age-specific fecundity:

$$F_x = (\alpha + \beta \cdot T)x \cdot e^{-(\delta + \epsilon T)x} \tag{8}$$

where F_x is the daily age-specific fecundity rate, T is temperature, x is the age, and α, β, δ, and ϵ are constants. For fitting the

age-specific fecundity at single temperature treatment (i.e., T is also a constant), $(\alpha + \beta\,T)$ and $(\delta + \epsilon\,T)$ can be simplified as constants a and b, respectively. Equation 8 can be simplified as

$$F_x = ax \cdot e^{-bx} \qquad (9)$$

In Enkegaard (1993), the adult age, i.e., the reproductive age (x) of newly emerged adult was indexed from zero, was used to fit the age-specific fecundity to Equation 8. Huang and Chi (2013) pointed out the problem of constructing life table based on adult age. To avoid the problem of using adult age, we modified Equation 9 to index the reproductive age from egg stage as

$$F_x = a(x - c) \cdot e^{-b(x-c)} \qquad (10)$$

where c is a parameter of reproductive age.

We also fitted the m_x curve to a 4-parameter Weibull function (Wahed et al. 2009, Almalki and Yuan 2013) using SigmaPlot version 12.5 (Systat Software, San Jose, CA) as

$$
M(x; x_0, a, b, c) =
\begin{cases}
0, \text{ if } x \le x_0 - b \times \left(\dfrac{c-1}{c}\right)^{\frac{1}{c}} \\[2ex]
a \times \left(\dfrac{c-1}{c}\right)^{\left(\frac{1-c}{c}\right)} \times \left| \dfrac{x - x_0}{b} + \left[\left(\dfrac{c-1}{c}\right)^{\frac{1}{c}}\right] \right|^{(c-1)} \\[2ex]
\times \exp\left\{ -\left| \left[\dfrac{x - x_0}{b} + \left(\dfrac{c-1}{c}\right)^{\frac{1}{c}}\right]^{c} \right| + \dfrac{c-1}{c} \right\}
\end{cases}
$$

$$(9)$$

where x_0, a, b, and c are model parameters.

Results

The aphid had four nymphal instars, and nymphs were able to complete their development from first instar to adult on all of the pear cultivars. The means of the developmental times for each nymphal stage and total preadult developmental period, as well as total immature mortality rates, of *D. pyri* for each of the four different pear cultivars are given in Table 1. Significant differences were found for the first and fourth nymphal stages of the aphids reared on the different cultivars; the duration of both of the stages was the shortest on Williams, while the duration of the first stage was the longest on Ankara and the longest fourth stage was on Coscia (Table 1). Total immature developmental times on Coscia and Ankara were similar and significantly longer than those on the other cultivars tested. Total preadult mortality was also higher on Coscia (19%) and Ankara (18%) cultivars than on Santa-Maria (12%), and Williams (11%) even though the differences were not statistically significant.

Feeding on different pear cultivars did not affect the reproductive period, but resulted in differences in the total prereproductive period (TPRP), fecundity, and adult longevity (Table 2). TPRP values obtained on Coscia and Ankara cultivars were considerably longer than those on Santa-Maria and Williams. The shortest reproductive period was on Ankara followed by Coscia, Williams, and Santa-Maria. Mean total fecundity on Ankara was significantly lower than that on Santa-Maria. Adults reared on Ankara lived significantly shorter than those reared on Santa-Maria.

The age-stage-specific survival rate (s_{xj}) is the probability that a newborn aphid will survive to age x and stage j (Fig. 1). The probability that a newly emerged nymph will survive to the adult stage was 0.81, 0.82, 0.88, and 0.89 for Coscia, Ankara, Santa-Maria,

and Williams, respectively. These curves also showed the survivorship and stage differentiation, which is an advantage of using the age-stage, two-sex life table. The overlapping between stages graphically illustrated the variable developmental rate among individuals (Fig. 1). Adult aphids emerged later and lived the shortest life span on Ankara. Adults emerged on Coscia, Ankara, Santa-Maria, and Williams cultivars at age 10, 11, 9, and 9 d, and survived 42, 26, 37, and 41 d, respectively (Fig. 2).

The m_x (the age-specific fecundity of total population) and $l_x m_x$ (age-specific maternity) peaks observed in Coscia and Ankara were similar and were lower than those obtained on Santa-Maria and Williams (Fig. 2). The l_x value is the probability that a newly emerged nymph will survive to age x and is calculated by pooling all surviving individuals of different stages. The l_x curve is a simplified version of the curves in Fig. 1.

The age-stage-specific life expectancy (e_{xj}) of *D. pyri* grown on different pear cultivars is plotted in Fig. 3. The life expectancy is the time that an individual of age x and stage j is expected to live. The life expectancy of a newborn nymph (e_{01}) is exactly the same as the mean longevity. Because this study was conducted entirely in clip-cells that prevented exposure to the adverse effects of field conditions, the life expectancy decreased gradually with aging.

The age-stage-specific reproductive value (v_{xj}) describes the contribution of an individual aphid of age x and stage j to the future population. The major peaks in reproductive values of females reared on Coscia, Ankara, Santa-Maria, and Williams cultivars were at 13 d ($v_{13} = 14.9$), 13 d ($v_{13} = 14.9$), 12 d ($v_{12} = 16.4$), and 12 d ($v_{11} = 16.2$), respectively (Fig. 4). The later and smaller v_{xj} peaks found on Coccia and Ankara indicates that the *D. pyri* population will increase slower on these cultivars, and the number of generations will be less than that on other cultivars.

The means and standard errors of the population parameters were estimated by employing the bootstrap technique (Table 3). The intrinsic rate of increase and finite rate of increase, which showed a similar trend, were lower, while the mean generation time was longer on Coscia followed by Ankara. The net reproductive rate was the lowest on Ankara followed by Coscia; however, differences among the cultivars tested were not significant.

The parameters obtained by fitting the survival rate (l_x) to 2-parameter Weibull distribution, and the fecundity data (m_x) to modified Enkegaard model and 4-parameter Weibull distribution are listed in Table 4.

Discussion

Because demographic parameters are capable of providing an accurate estimate of the growth rate of an insect pest population, a thorough understanding of these parameters is essential in developing ecologically sound pest management strategies and programs. It is, therefore, crucial to accurately calculate these parameters. When using the age-stage, two-sex life table, data of all individuals, including female, male, and those died in the preadult stage, were included. Thus, it incorporates the variable developmental rate among individuals and accurately describes the stage differentiation. In this study, although the subject insects are parthenogenetic, the use of the age-stage, two-sex life table enables the description of stage differentiation as shown in Figs. 1, 3, and 4. These features would not have been observed if the female age-specific life table were used. Moreover, as the application of jackknife method has been proved inadequate for life table analysis (Huang and Chi 2012, Huang and Chi 2013, Yu et al. 2013), we used the bootstrap

Table 1. Developmental time (mean ± SE) and preadult survival rate of *D. pyri* reared on four different pear cultivars

Cultivars		Duration of developmental stages (d)					Preadult survival rate (%)
	n	First instar	Second instar	Third instar	Forth instar	Total preadult	
Coscia	42	2.5 ± 0.19ab	2.8 ± 0.23a	3.1 ± 0.18a	4.2 ± 0.27a	12.7 ± 0.43a	0.81 ± 0.09a
Ankara	34	2.8 ± 0.16a	2.7 ± 0.13a	3.1 ± 0.18a	3.9 ± 0.18ab	12.6 ± 0.29a	0.82 ± 0.09a
Santa-Maria	34	2.3 ± 0.14ab	2.4 ± 0.12a	2.9 ± 0.19a	3.7 ± 0.16ab	11.3 ± 0.32b	0.88 ± 0.08a
Williams	36	2.1 ± 0.10b	2.8 ± 0.17a	3.0 ± 0.22a	3.3 ± 0.28b	11.1 ± 0.30b	0.89 ± 0.07a

Means followed by different letters in the same column are significantly different between cultivars determined by using the paired boostrap test. Standard errors were estimated by using 200,000 bootstraps.

Table 2. The total prereproductive period (TPRP), reproductive period, fecundity, and longevity of *D. pyri* reared on different pear cultivars (mean ± SE)

Cultivars	TPRP (d)	Reproductive period (d)	Fecundity (nymphs/female)	Adult longevity (d)
Coscia	14.12 ± 0.38a	14.8 ± 1.68a	42.1 ± 6.63ab	20.6 ± 2.01ab
Ankara	13.90 ± 0.40a	13.6 ± 1.43a	37.4 ± 3.78b	18.1 ± 1.49b
Santa-Maria	12.50 ± 0.39b	17.3 ± 1.32a	49.7± 4.69a	22.6 ± 1.68a
Williams	12.56 ± 0.34b	15.9 ± 1.71a	49.1 ± 6.39ab	20.9 ± 2.11ab

Means followed by different letters in the same column are significantly different between cultivars determined by using the paired bootstrap test. Standard errors were estimated by using 200,000 bootstraps.
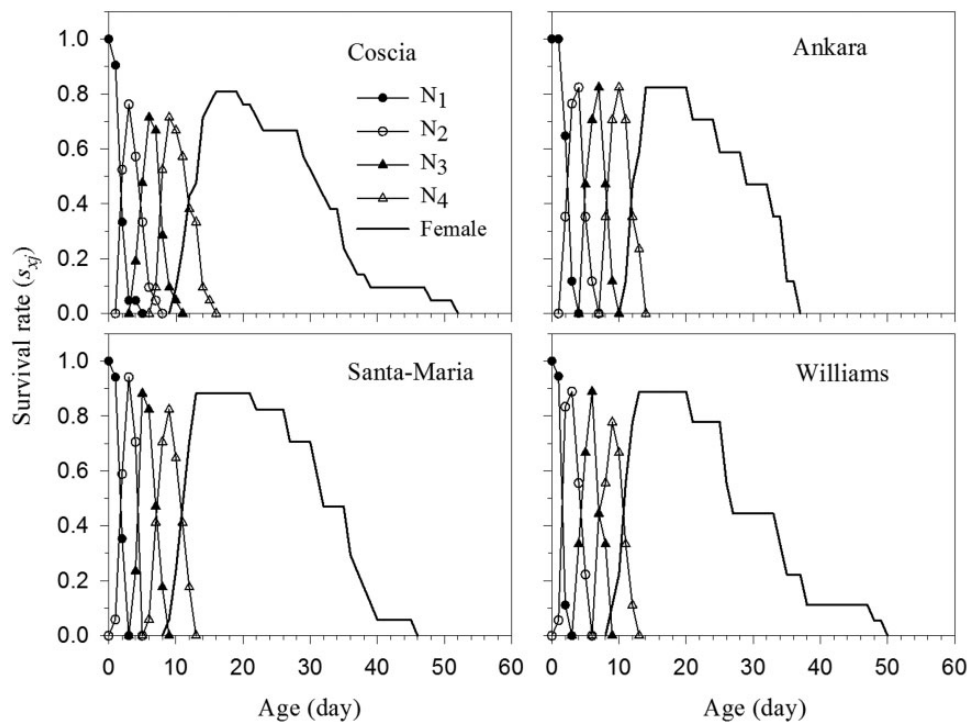
Fig. 1. Age-stage survival rate (s_{xj}) of *D. pyri* on four different pear cultivars.

technique with 200,000 resampling to obtain precise estimate of population parameters. In bootstrapping, the standard errors are estimated by using the means of all resampling ($n = 200,000$). Because 200,000 bootstraps generated a normal frequency distribution which is essential for the variance analysis and comparison, the results of statistical test were not caused by the variation in developmental times due to sample sizes (Polat-Akköprü et al. 2015).

This study was carried out in field conditions. Life table study under controlled laboratory conditions reveal the biological

potential of the development and fecundity of insect populations. In natural environments, however, most populations are influenced by a variety of changing factors like temperature and humidity. Insects are ectothermic, and their body temperature, development, survival, fecundity, longevity, and eventually population growth are affected by their surrounding temperature. Because of fluctuating temperature in field, population parameters that reflect combined effects of immature development, survival rate, fecundity, and longevity under field environments can be different from the constant
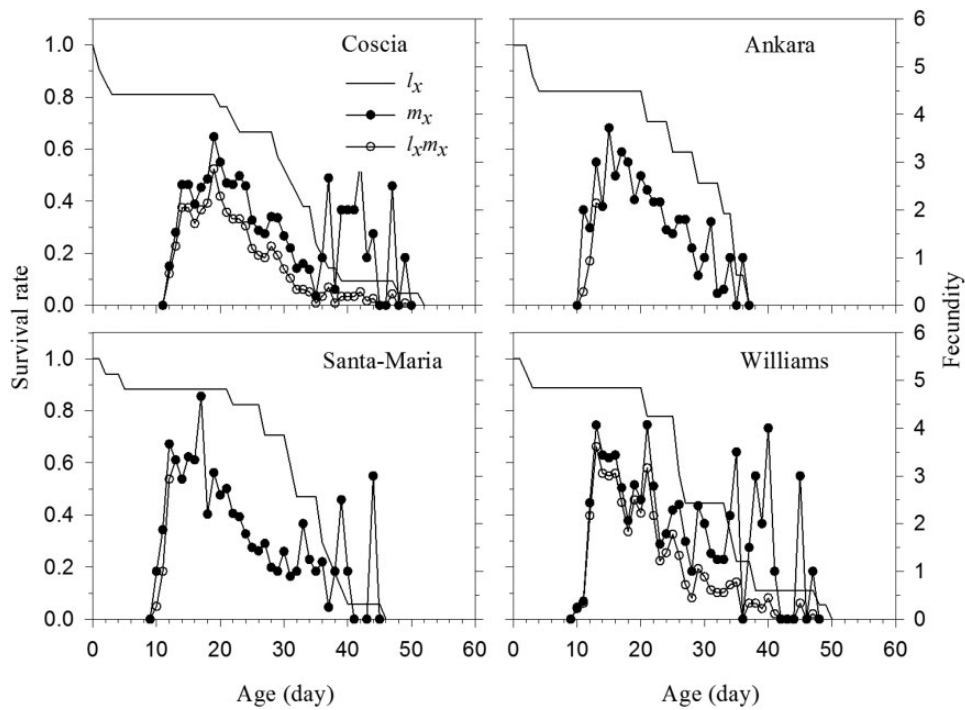
Fig. 2. Age-specific survival rate (l_x), fecundity (m_x), and net maternity ($l_x m_x$) of *D. pyri* on four different pear cultivars.
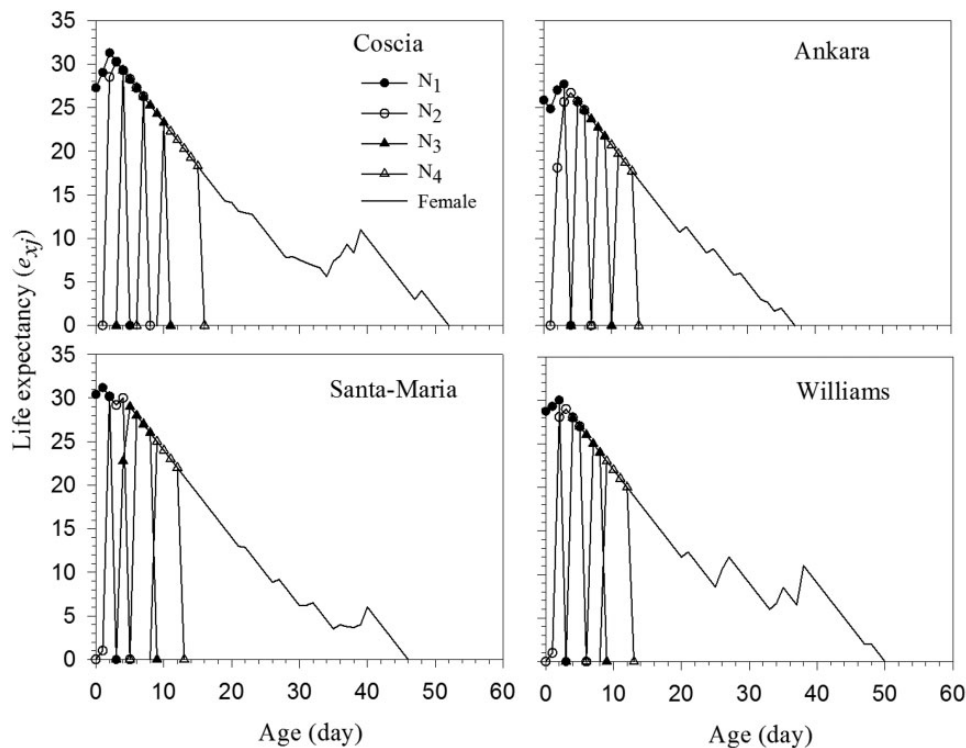

Fig. 3. The age-stage life expectancy (e_{xj}) of *D. pyri* on four different pear cultivars.

laboratory conditions as shown in the studies on population growth of *Sipha flava* (Auad et al. 2015), *Aphis gossypi* (Hosseini-Tabesh et al. 2015), and *A. craccivora* (Jalalipour et al. 2017). These differences show the necessity of collecting life tables under both constant and fluctuating temperatures. The life tables under constant temperatures can reveal the growth

potential of insect populations and are repeatable, whereas the life tables under field condition demonstrate the variability of population growth and are important information for practical pest management.

The results obtained in this study revealed that feeding on different pear cultivars affected the population growth rate of the *D. pyri*
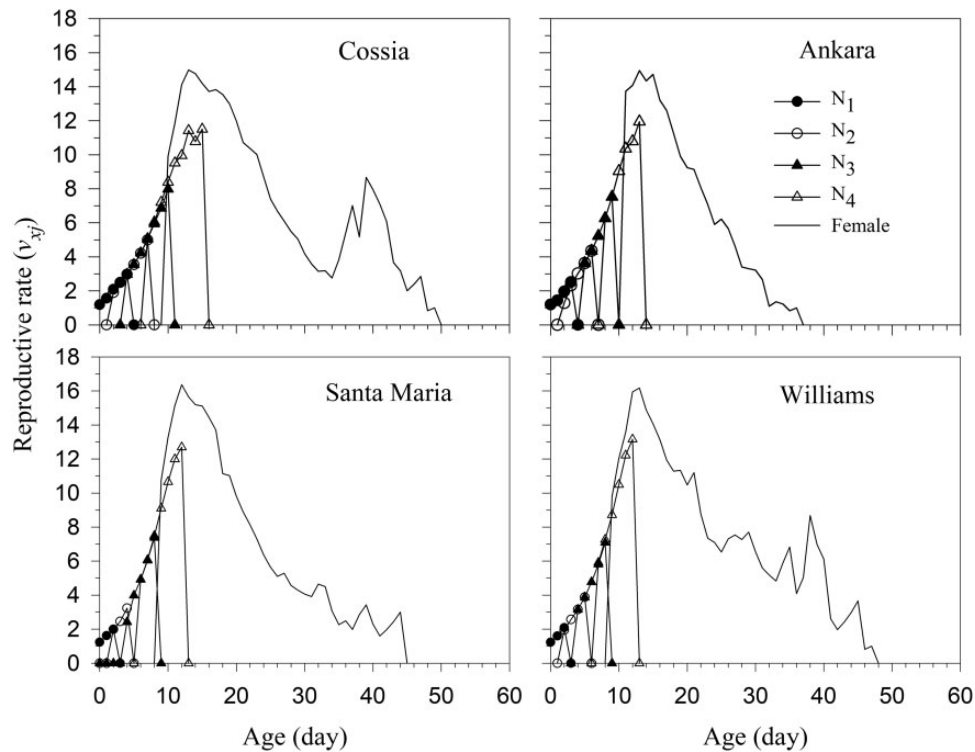
Fig. 4. Age-stage reproductive value (v_{xj}) of *D. pyri* on four different pear cultivars.

Table 3. Population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproductive rate; T, mean generation time) of *D. pyri* reared on different pear cultivars (mean $\pm$ SE)

Cultivars	r (d^{-1})	λ (d^{-1})	R_0 (offspring)	T (d)
Coscia	0.1760 ± 0.0099c	1.1923 ± 0.0118c	34.1 ± 6.46a	20.1 ± 0.59a
Ankara	0.1824 ± 0.0099bc	1.2001 ± 0.0120bc	30.8 ± 4.64a	18.8 ± 0.63ab
Santa-Maria	0.2095 ± 0.0094a	1.2330 ± 0.0116a	43.8 ± 5.65a	18.0 ± 0.47b
Williams	0.2063 ± 0.0073ab	1.2290 ± 0.0089ab	43.7 ± 6.75a	18.3 ± 0.67b

Table 4. Estimated regression parameters of age-specific survival rate curves (l_x) (fitted to Weibull frequency distribution) and age-specific fecundity (m_x) (fitted to Weibull-4 parameters model and modified Enkegaard model) for *D. pyri* reared on different pear cultivars

Model	Parameter	Coscia	Ankara	Santa-Maria	Williams
Weibull model for age-specific survival rate	b	32.552 (0.639)	30.736 (0.513)	34.727 (0.334)	32.517 (0.378)
	c	2.673 (0.194)	3.367 (0.254)	4.650 (0.271)	3.146 (0.156)
	R^2	0.937	0.9555	0.980	0.979
Modified Enkegaard model (ME; for age-specific fecundity)	a	2.254 (0.818)	6.868 (1.500)	5.240 (1.185)	2.114 (0.765)
	b	10.312 (0.900)	10.409 (0.235)	9.281 (0.314)	8.806 (0.897)
	c	0.106 (0.012)	0.163 (0.010)	0.149 (0.010)	0.104 (0.013)
	R^2	0.4486	0.8245	0.7592	0.4021
Weibull-4 parameters model (for age-specific fecundity)	a	2.594 (0.190)	2.982 (0.097)	3.415 (0.213)	3.193 (0.248)
	b	19.222 (1.960)	10.886 (0.393)	13.081 (0.927)	18.576 (1.960)
	c	1.271 (0.102)	1.428 (0.061)	1.190 (0.109)	1.203 (0.090)
	x_0	17.657 (1.596)	16.531 (0.400)	14.217 (0.711)	15.222 (1.588)
	R^2	0.6861	0.9359	0.8742	0.6919

primarily due to the differences that occurred in the immature developmental time, survival rate, and fecundity and, consequently, the differences in the population parameters (r, λ, R_0, and T). Other reports on effects of host plants on the population growth of various species of aphids are in agreement with the results described here (Ruggle and Gutierrez 1995, Tsai 1998, Tang et al. 1999, Yue and Liu 2000, Kazemi et al. 2001, Özgökçe and Atlihan 2005, Kaydan

et al. 2006, Polat-Akköprü et al. 2015). Host choice and acceptance by aphids are directly related to morphological, nutritional, and biochemical features of the host plants (Thompson 1988, Bernays and Chapman 1994, Dixon 1998). Differences in the immature developmental time, survival rate, and fecundity on different pear cultivars may reflect the suitability of the food substrate, i.e., sap quality and the proportions of essential nutrients. Because sucking insects will
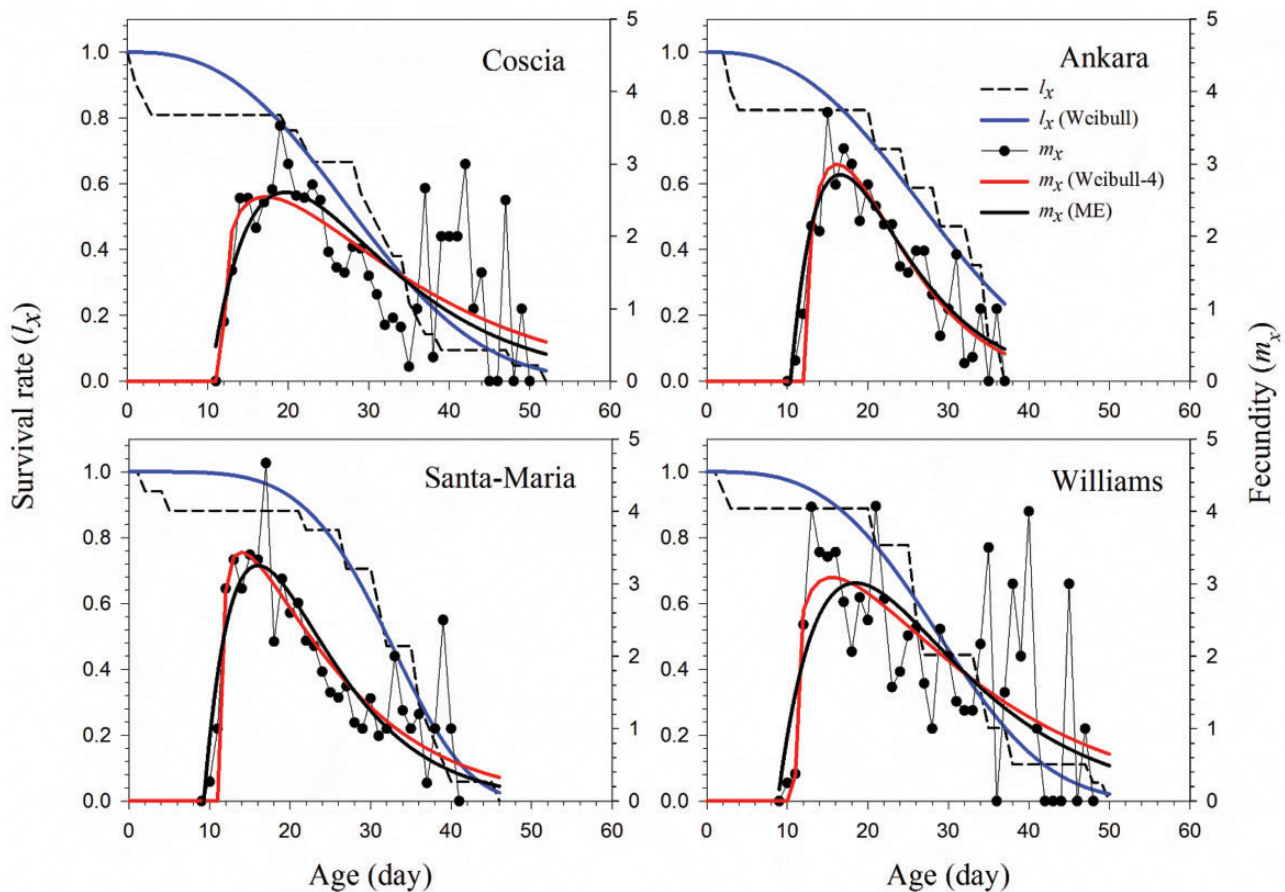
Fig. 5. Observed and fitted curves of l_x and m_x. The l_x curves were fitted to 2-parameter Weibull function. The m_x curves were fitted to 4-parameter Weibull function and modified Enkegaard (ME) model.

have impaired reproduction and produce few offspring when fed on host plant leaves containing low levels of soluble nitrogen, fecundity is an ideal biological parameter for demonstrating the quality of a particular host by measuring the reproductive success of the pest insect (Awmack and Leather 2002). A plant reacts to an insect attack by increasing protein synthesis and gene expression that results in activation of the plant's defensive mechanisms (Smith 2005). For example, in cultivars that are less suitable for the pest, the attacked plant may increase production of chlorophyll or protein to overcome the losses caused by the pest attack, triggering the processes of resistance (Bernardi et al. 2012).

On the other hand, performance of the aphids may also be affected by trichome density on the surface of the pears leaves. Adverse effects due to densities of glandular and nonglandular trichomes on aphids have been reported (Greer and Nielsen 1988, Severson et al. 1992). It has been indicated that glandular trichomes produce alkaloids, diterpenes, and sugar esters that are highly effective against phytophagous insects, including aphids (Thurston et al. 1966, Thurston 1970).

Population parameters, i.e., the intrinsic rate of increase (r), finite rate of increase (λ), and net reproductive rate (R_0), are appropriate indicators for measuring the effect of a host plant on the development, survival, and fecundity of a population. Each of these parameters was found to be lower on the Coscia and Ankara cultivars. The lower values on these cultivars were due to several factors, including extended preadult developmental times, lower survival rates to adulthood, lower daily rates of

offspring production, and delayed peaks in reproduction. Even a small reduction in these parameters can ultimately cause considerable change in a pest's population size (Goundoudaki et al. 2003). Such reductions in the aphid populations caused by resistant or less favorable cultivars may also enhance the effectiveness of natural enemies in controlling *D. pyri* populations on pear trees (Goundoudaki et al. 2003)

According to our results, Coscia and Ankara are less favorable or more tolerant hosts for development and reproduction of bedstraw aphids. Slower development and population growth on these cultivars may allow the pear trees more opportunity to compensate for damage caused by the aphids and reduce the need for insecticide applications. Using tolerant varieties, however, may not be enough to keep the aphid population under the economic threshold, although it may create a less favorable environment for the aphid population growth rate. The findings obtained from this study should be taken into consideration when designing integrated management schemes for controlling *D. pyri* on pear trees, and can also be used in population studies to design and evaluate control strategies.

Fitting observed survival and fecundity data to models has been widely attempted in some life table research and temperature-dependent developmental rate. The most widely used function for the survival curve is the Weibull function (Zahiri et al. 2010). For the fecundity curve, the Enkegaard model (Enkegaard 1993, Zahiri et al. 2010), Bieri model (Lanzoni et al. 2004), and polynomial model (Pervez and Omkar 2004) have been used. Weibull

distribution has been widely used in industry, environmental science, and biological sciences to describe "time-to-failure" or survival probability. In industrial applications, the expected values obtained from Weibull regression are mostly consistent with the observed values because of the standardized production in industry. The Weibull distribution also fits well with observed data in human longevity studies as a result of improvements in medical care, where human mortality is now mainly due to aging. The Weibull-fitted curves of insect survival rates, however, often show significant differences. Due to the stage-structured life history that is characteristic of insects, some stages are more sensitive to various mortality factors, while other stages are little, if at all, affected by the same factors. Because insects are ectothermic organisms, their stage-specific survival is affected differently by changing temperatures. Therefore, dramatically higher mortalities are often observed in some stages, while the survival rate declines gradually in other stages. The Weibull-fitted survival curves often show significant deviation from the observed ones for some age durations where a higher stage-specific mortality has occurred. This stage-specific higher mortality is not observable in traditional age-specific life tables, because they ignore stage differentiation and are not able to precisely describe the stage survival rate (Huang and Chi 2012).

The original model of Enkegaard (1993) was developed based on adult age and the preadult duration was ignored. As Lewontin (1965) demonstrated the importance of the age of first reproduction, inclusion of the preadult duration is important in fitting age-specific fecundity curve (m_x) and Huang and Chi (2013) pointed out the problem of constructing life table based on adult age. In this paper, we modified the Enkegaard model to take the preadult duration into consideration. However, because the age-specific fecundity mostly showed significant fluctuation or periodic oogenesis (i.e., insects laying egg mass or ootheca; Tsai and Chi 2007), fitting fecundity curve and applying the fitted curve should be practiced with caution.

Moreover, life table itself is a theory and the survival rate and fecundity are closely correlated to each other as in the net reproductive rate (equation 3), Euler–Lotka equation (equation 4), and the reproductive value (equation 6). Fitting only the survival curve (l_x) to the Weibull function or only the fecundity curve (m_x) to any of the above mentioned model should be practiced with caution. The biological meaning of the fitted function should be critically examined. As Tuan et al. (2016) pointed out, there may be a problem with fitting a survival curve to the Weibull distribution. A similar situation can be seen in Fig. 5, where the fitted curves could not precisely describe the observed data. If the fitted survival and fecundity data were used in the simulation, the simulated population size would be wrong, because there was high mortality during the nympal stage, while the fitted one (Weibull) would have predicted low mortality in this situation. Because no solid biological meaning and reasoning have been given to the parameters of models, such kind of curve fitting should be applied with caution.

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