

# Demographic Assessment of Plant Cultivar Resistance to Insect Pests: A Case Study of the Dusky-Veined Walnut Aphid (Hemiptera: Callaphididae) on Five Walnut Cultivars

EVIN POLAT AKKÖPRÜ,<sup>1</sup> REMZI ATLIHAN,<sup>1,2</sup> HAYRETTIN OKUT,<sup>3</sup> AND HSIN CHI<sup>4</sup>

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**ABSTRACT** To provide a comprehensive evaluation of walnut cultivar resistance to the dusky-veined walnut aphid, *Panaphis juglandis* (Goeze), we collected the life table data of this aphid reared on five cultivars of walnut ('Akça I,' 'Chandler,' 'Fernette,' 'Femor,' and 'Pedro') under field conditions. The raw data of the developmental time, survival rate, and fecundity was analyzed using the age-stage, two-sex life table to account for the variable developmental rate and stage differentiation among individuals. Due to the species' longer immature developmental time, shorter adult longevity, shorter reproduction period, and lower fecundity, the net reproduction rate ( $R_0 = 5.9$  offspring), intrinsic rate of increase ( $r = 0.0983 \text{ d}^{-1}$ ), and finite rate ( $\lambda = 1.1034 \text{ d}^{-1}$ ) were the lowest when aphids were reared on the Femor cultivar, while those reared on Akça I exhibited the highest population parameters ( $R_0 = 18.0$  offspring,  $r = 0.2031 \text{ d}^{-1}$ , and  $\lambda = 1.2252 \text{ d}^{-1}$ ). Based on the population characteristics, Femor is a less favorable cultivar for the development and reproduction of *P. juglandis*. We also demonstrated the advantages of using bootstrapping for the analysis of standard errors of developmental time, longevity, fecundity, and other parameters as well. Our results indicated that demographic analysis of pest development, survival, and reproduction based on the age-stage, two-sex life table offers a comprehensive assessment of pest growth potential on different crop cultivars.

**KEY WORDS** *Panaphis juglandis*, walnut cultivar, life table

Turkey is one of the top five walnut-producing countries (Anonymous 2011a), with the Lake Van basin being one of the most important regions of walnut production in Turkey (Anonymous 2012). The dusky-veined aphid, *Panaphis juglandis* (Goeze) (Hemiptera: Callaphididae) is one of the major pests in the Lake Van basin, causing damage to walnuts especially in early summer (Atlihan et al. 2011). This species is common throughout Europe (Heie 1992, Barbagallo et al. 1995, Nieto Nafria and Durante 1998, Petrović 1998), Central Asia, and the United States (Blackman and Eastop 2000, Anonymous 2011b). When a walnut tree is infested with this aphid, both the nut size and quality may decrease (University of California 2011). In the Lake Van basin, pesticides are usually applied to suppress the aphid population in walnut orchards in early summer. The application of pesticides may, however, not only add extra costs and cause residuals problem but also negatively impact natural biological control agents. For an ecological and

economic pest control program, use of resistant or less-favorable crop cultivars is considered one of the major components of integrated pest management (Özgökçe and Atlihan 2005). Walnut trees in the Lake Van basin are primarily grown from seed. Therefore, it is especially important to select resistant or nonpreferred cultivars at the beginning of a breeding program. However, no information is currently available regarding the interaction between dusky-veined walnut aphids and resistant walnut cultivars. Because the life table provides the most comprehensive description of development, survival, and reproduction, it is an essential tool for assessing the viability of insects. In this study, life table data (i.e., development, stage differentiation, survival, and fecundity) of the dusky-veined walnut aphid on five popular walnut cultivars was collected. We then analyzed the data using the age-stage, two-sex life table to reveal the differences in the population parameters. This information will be valuable for pest management in the walnut production system.

## Materials and Methods

The walnut cultivars used for experiments were 'Akça I,' 'Chandler,' 'Fernette,' 'Femor,' and 'Pedro.' *P. juglandis* adults were collected from walnut orchards in the Lake Van basin and reared for a generation on

<sup>1</sup> Department of Plant Protection, Faculty of Agriculture, University of Yuzuncu Yil, 65080 Van, Turkey.

<sup>2</sup> Corresponding author, email: ratlihan@yyu.edu.tr.

<sup>3</sup> Department of Animal Sciences, Faculty of Agriculture, University of Yuzuncu Yil, 65080 Van, Turkey.

<sup>4</sup> Laboratory of Theoretical Ecology, Department of Entomology, National Chung Hsing University, Taichung, Taiwan, Republic of China.

potted walnut plants of each cultivar (pot size: 90 cm in diameter and 90 cm in height) kept in an experimental orchard of the Agriculture Faculty of Yuzuncu Yil University. Soil, sandy loam, was taken from the experimental orchard of the Agriculture Faculty of Yuzuncu Yil. Manure (120 g per pot) was added to the soil for fertilization at the beginning of study. Plants were watered once a week. For the life table study, adults were transferred onto a leaf individually and kept in a Plexiglas clip-cell (20 by 10 mm with their upper side covered by muslin). After 12 h, one newborn nymph was kept in each cell, and other newborn nymphs and adults were removed. On each plant, only three to four leaf cages were used. The developmental stage and survival were observed daily. After the emergence of an adult, the number of newborn nymphs was recorded and removed from the cell daily until the death of the adult. The numbers of individuals ( $n$ ) used at the beginning of the life table study were 60, 42, 41, 39, and 42 newborns for Akça I, Chandler, Fernette, Fernor, and Pedro, respectively. All treatments were conducted during the same period (June and July, 2011). During the experimental period, the average temperature was 21.2°C (ranged from 19.2 to 23.1°C), average relative humidity was 42.8% (ranged from 39.6 to 45.9%), and photoperiod was 14:10 (L:D) h.

**Data Analysis.** The raw data of developmental time, survival, and daily fecundity of all individuals was analyzed using an age-stage, two-sex life table to take into account the variable developmental rate among individuals (Chi and Liu 1985, Chi 1988). Following the methods of Chi and Liu (1985), the age-stage-specific survival rate ( $s_{xj}$ ) (where  $x$  is the age and  $j$  is the stage), age-stage-specific fecundity ( $f_{xj}$ ) of female adults, age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), and population parameters ( $R_0$ , net reproductive rate;  $r$ , intrinsic rate of increase;  $\lambda$ , finite rate of increase;  $T$ , mean generation time) were calculated. The value of  $s_{xj}$  is the probability that a newborn nymph will survive to age  $x$  and stage  $j$ . The value of  $l_x$  is the probability that a newborn nymph will survive to age  $x$  and is calculated by pooling all of the surviving individuals of different stages. It is calculated as

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

where  $\delta$  is the last stage of the study cohort. The  $m_x$  was calculated using the following equation:

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

The cumulative net reproductive rate ( $R_x$ ) was calculated as follows:

$$R_x = \sum_{y=0}^x l_y m_y \tag{3}$$

The net reproductive rate  $R_0$  is the cumulative summation of  $l_x m_x$  from birth to death and is calculated as

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{4}$$

The intrinsic rate of increase was estimated using the iterative bisection method from the Euler-Lotka formula:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{5}$$

With age indexed from 0 (Goodman 1982). The finite rate of increase was calculated as

$$\lambda = e^r \tag{6}$$

The mean generation time is defined as the length of time that a population requires to increase to the  $R_0$ -fold of its size (i.e.,  $e^{rT} = R$  or  $\lambda^T = R_0$ ) at the stable age-stage distribution. It is calculated as follows:

$$T = \frac{\ln R_0}{r} \tag{7}$$

Based on the age-stage, two-sex life table, the life expectancy ( $e_{xj}$ ) was calculated according to Chi and Su (2006) and defined as the time that an individual of age  $x$  and stage  $j$  is expected to live. The age-stage-specific reproductive value ( $v_{xj}$ ) for an individual of age  $x$  and stage  $j$  was calculated according to Tuan et al. (2014). The standard errors of the developmental times, fecundity, reproduction period, and population parameters were estimated using the bootstrap technique (Efron and Tibshirani 1993, Huang and Chi 2012b). To obtain stable estimates, we used 40,000 bootstraps ( $B$ ). The differences among the cultivars were compared using the paired bootstrap test. A user-friendly computer program, TWSEX-MSChart, was used to estimate the parameters (Chi 2014); routines for both the bootstrap and paired bootstrap test were included in it. The TWSEX-MSChart is available at <http://140.120.197.173/ecology/Download/TWSEX-MSChart.rar>.

**Results**

The means of the developmental times for each nymphal stage and the total preadult developmental

**Table 1. Developmental time (mean  $\pm$  SE) of the first to fourth nymphal stages (N1, N2, N3, and N4) and preadult mortality of *P. juglandis* reared on different walnut cultivars**

Cultivars	n	Developmental time (d)					Preadult survival rate (%)
		N1	N2	N3	N4	Total preadult	
Akça I	52	3.12 $\pm$ 0.04b	2.56 $\pm$ 0.08b	3.27 $\pm$ 0.08b	1.96 $\pm$ 0.09c	10.81 $\pm$ 0.11c	86.6 $\pm$ 4.4a
Chandler	33	2.93 $\pm$ 0.04c	2.12 $\pm$ 0.07d	3.27 $\pm$ 0.10b	3.03 $\pm$ 0.10ab	11.33 $\pm$ 0.11b	78.5 $\pm$ 6.3a
Fernette	34	3.37 $\pm$ 0.08a	2.34 $\pm$ 0.07c	3.03 $\pm$ 0.11b	2.97 $\pm$ 0.10a	11.59 $\pm$ 0.16b	82.9 $\pm$ 5.9a
Fernor	30	3.51 $\pm$ 0.09a	4.13 $\pm$ 0.09a	4.44 $\pm$ 0.12a	2.71 $\pm$ 0.16b	14.55 $\pm$ 0.23a	79.5 $\pm$ 6.5a
Pedro	36	2.71 $\pm$ 0.11c	2.71 $\pm$ 0.11b	3.02 $\pm$ 0.13bc	3.08 $\pm$ 0.10a	11.58 $\pm$ 0.14b	85.7 $\pm$ 5.4a

The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same column are significantly different between cultivars using the paired bootstrap test at 5% significance level.

**Table 2. Reproduction period, fecundity, adult longevity, and mean longevity of *P. juglandis* reared on different walnut cultivars (mean  $\pm$  SE)**

Cultivars	Reproduction period (d)	Fecundity (nymphs/female)	Adult longevity (d)	Mean longevity (d)
Akça I	5.67 $\pm$ 0.32a	20.79 $\pm$ 1.38a	7.75 $\pm$ 0.43a	17.30 $\pm$ 0.57ab
Chandler	4.41 $\pm$ 0.43b	19.09 $\pm$ 2.20a	6.18 $\pm$ 0.63b	15.51 $\pm$ 0.81c
Fernette	4.22 $\pm$ 0.33b	11.38 $\pm$ 1.19b	7.79 $\pm$ 0.51a	17.93 $\pm$ 0.69a
Fernor	3.38 $\pm$ 0.27c	7.42 $\pm$ 1.01c	5.74 $\pm$ 0.39b	18.62 $\pm$ 0.67a
Pedro	3.54 $\pm$ 0.34c	13.17 $\pm$ 1.60b	5.50 $\pm$ 0.47b	16.14 $\pm$ 0.56bc

The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same column are significantly different between cultivars using the paired bootstrap test at 5% significance level.

period, as well as the total immature mortality rates of *P. juglandis* reared on five different walnut cultivars, are presented in Table 1. The developmental times of the first nymphal stage for aphids reared on the five cultivars were significantly different from each other. In general, the developmental times of the nymphal stages for *P. juglandis* reared on Fernor were longer than those reared on other cultivars, except the fourth nymphal stage. The total immature duration of *P. juglandis* reared on Fernor was significantly longer than those reared on other cultivars. The shortest developmental time was observed on Akça I. The highest immature survival rate (86.6 %) of *P. juglandis* was observed on Akça I, while the lowest was on Chandler (78.5%); there were, however, no significant differences among the cultivars.

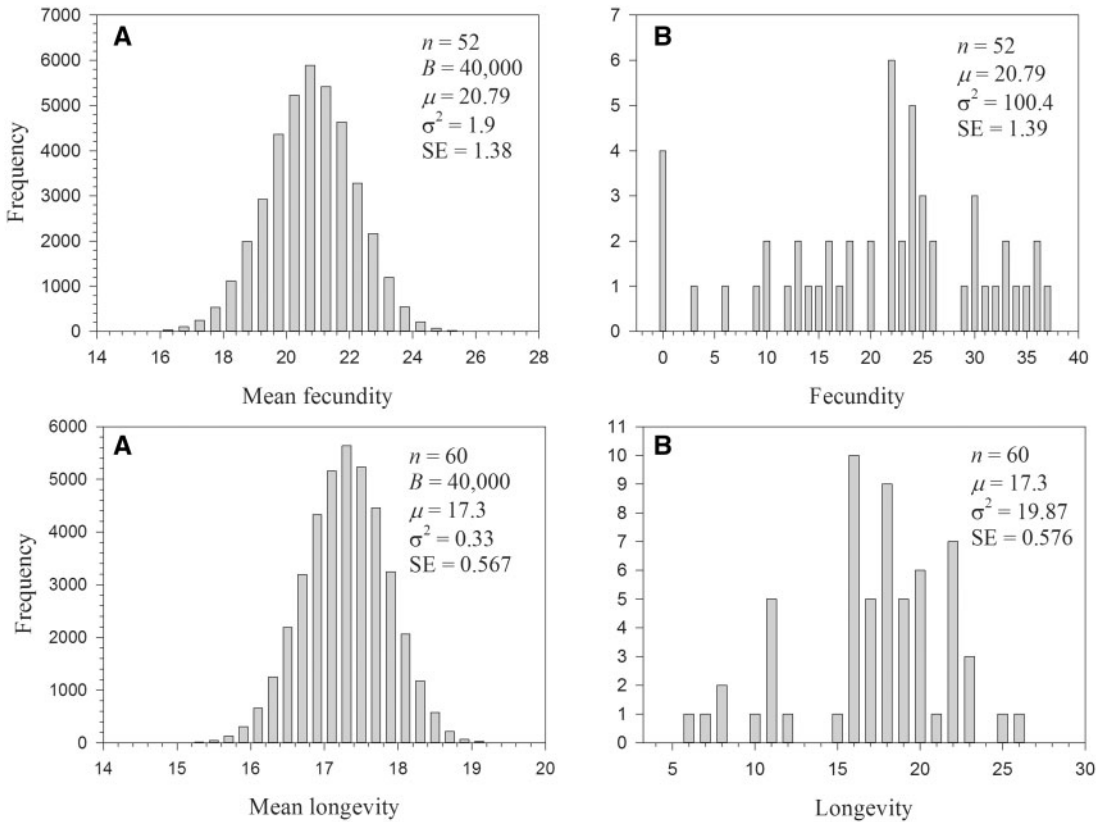
Feeding on different walnut cultivars resulted in differences in the reproduction period, fecundity, and adult longevity (Table 2). The shortest reproduction period and the lowest fecundity were observed on Fernor, while the longest reproduction period and highest fecundity were observed on Akça I. The adult longevity on Akça I and Fernette was significantly longer than that of the other three cultivars.

In this study, we used bootstrapping to calculate not only the standard errors (SE) of estimates of the population parameters but also the SE of developmental time, longevity, and fecundity. Because the bootstrap method is new to most entomologists, we used the data of *P. juglandis* reared on Akça I to show the difference between the standard statistical procedures and the bootstrap technique (Fig. 1). In general statistics, the SE is estimated by using data of all individuals in a cohort ( $n=60$  for longevity and 52 for fecundity). In bootstrapping, the SE is estimated by using the

means of all resampling ( $B=40,000$ ). Although the estimated SE is almost the same, bootstrapping generated a normal frequency distribution, which is essential for the following analysis and comparison. The bootstrap results were also consistent with the definition of the Central Limit Theorem: "As the sample size increases, the means of samples drawn from a population of any distribution will approach the normal distribution."

The age-stage-specific survival rate ( $s_{xy}$ ) (Fig. 2) of *P. juglandis* showed the probability that a newly born nymph will survive to each age-stage unit. The highest  $s_{xy}$  for the curve of adult stage was 0.82, 0.71, 0.83, 0.71, and 0.81 for Akça I, Chandler, Fernette, Fernor, and Pedro, respectively. These data seem different from the preadult survival rates of 86.6, 78.5, 82.9, 79.5, and 85.7%, respectively (Table 1). The seeming inconsistency was because some adults emerged earlier but died before other adults emerged. All of the data in Table 1 and Figure 2 are correct. These curves revealed not only the survivorship but also the stage differentiation, which is an important feature of insects. Overlapping between stages revealed the variable developmental rate among individuals. Adults of *P. juglandis* emerged later and survived for a shorter time on Fernor (Fig. 2).

The lowest peaks of  $m_x$  (the age-specific fecundity of the total population) and  $l_x m_x$  (the age-specific maternity) were observed on Fernor (Fig. 3). According to Equation 1, the curve of  $l_x$  is a simplified version of the curves shown in Figure 3. Because the net reproductive rate is the summation of  $l_x m_x$  from age zero to the death of the cohort, i.e.,  $R_0 = \sum_{x=0}^{\infty} l_x m_x$ , the curve of the cumulative net reproductive rate, i.e.,



**Fig. 1.** Frequency distribution of fecundity and longevity estimated using the bootstrap technique (A) and general statistics (B) ( $n$  = number of individuals,  $B$  = number of bootstraps).

$R_x = \sum_{y=0}^x l_y m_y$ , approaches the net reproductive rate of the respective cultivar (Fig. 3 and Table 3) when  $x$  approaches the last age of reproduction.

The age-stage-specific life expectancy ( $e_{xj}$ ) of *P. juglandis* on different walnut cultivars is plotted in Figure 4. The life expectancy of a newborn nymph ( $e_{01}$ ) is exactly the mean longevity. Because this study was conducted using Plexiglas clip-cells, which prevented the adverse effects of field conditions, the life expectancy decreased gradually with aging.

The age-stage-specific reproductive value ( $v_{xj}$ ) of *P. juglandis* describes the contribution of an individual of age  $x$  and stage  $j$  to the future population. The peak of the reproductive values of females reared on Akça I was 14.24 and occurred at age 11 d, while the peak of the reproductive values for Fernor was only 6.7 and occurred at a later age of 14 d (Fig. 5). The later peak of  $v_{xj}$  on Fernor indicates that the *P. juglandis* population will increase much slower on this cultivar.

The means and standard errors of the population parameters estimated using the bootstrap techniques are listed in Table 3. The net reproductive rate, intrinsic rate of increase, and finite rate of increase (which exhibited a similar trend) were lower, and the mean generation time was longer on Fernor in comparison with those of the other cultivars.

### Discussion

Metamorphosis, i.e., stage differentiation, is an important feature of insects and mites. By using the age-stage, two-sex life table, the emergence of each stage and overlaps between stages could be properly described in Figure 2. However, when the traditional female age-specific life tables are used, it is impossible to show the stage structure, and thus, it is impossible to describe the stage differentiation properly. Moreover, as Huang and Chi (2012a) noted, ignoring stage differentiation often results in the use of “adult age,” which consequently results in errors in  $l_x$  and  $m_x$  curves. Our study demonstrated that even for a parthenogenetic female population, it is advantageous to use the age-stage, two-sex life table to take the stage differentiation into consideration.

Our results revealed that the population growth rate of *P. juglandis* was affected by walnut cultivars because of the differences in the immature developmental time, reproduction period, and fecundity and, consequently, the differences in the population parameters ( $r$ ,  $\lambda$ ,  $R_0$ , and  $T$ ). Our findings are in agreement with many studies on the effects of host plants on development, survival, and reproduction of aphids (Ruggle and Guitierrez 1995, Tsai 1998, Satar et al. 1999, Tang et al. 1999, Yue and Liu 2000, Kazemi et al. 2001, Satar and

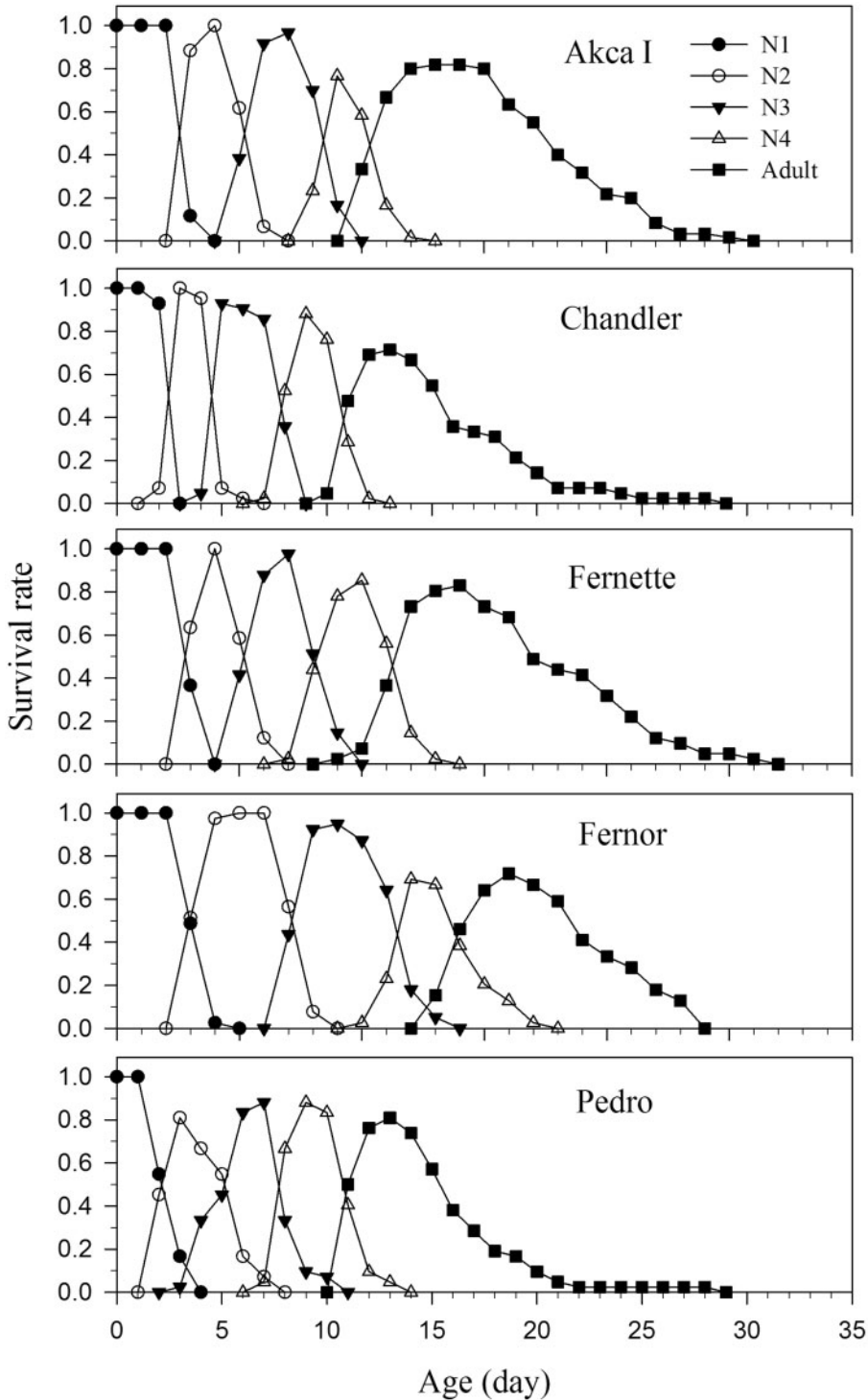
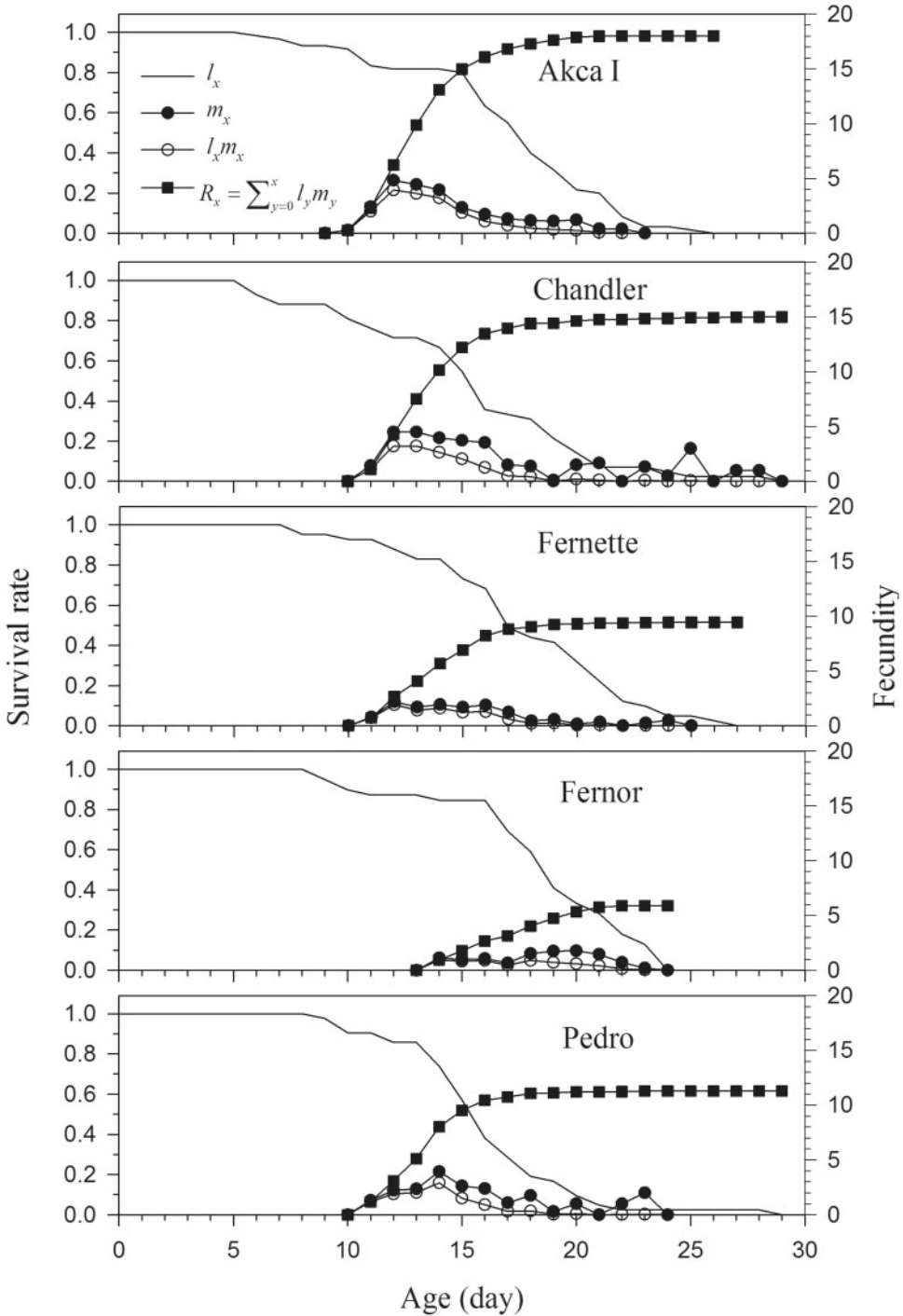


Fig. 2. Age-stage-specific survival rate ( $s_{xj}$ ) of *P. juglandis* reared on five walnut cultivars.

Yakomi 2002, Özgökçe and Atlıhan 2005). Plants play important roles in the host choice and the acceptance by aphids with their morphological, nutritional, and biochemical features (Thompson 1988, Bernays and

Chapman 1994, Dixon 1998). The differences in the immature developmental time, reproduction rates, and survival rates of *P. juglandis* may be attributed to nutrition and other chemicals in walnut leaves due to the



**Fig. 3.** Age-specific survival rate ( $l_x$ ), age-specific fecundity ( $m_x$ ), and age-specific maternity ( $l_x m_x$ ) of *P. juglandis* reared on five walnut cultivars.

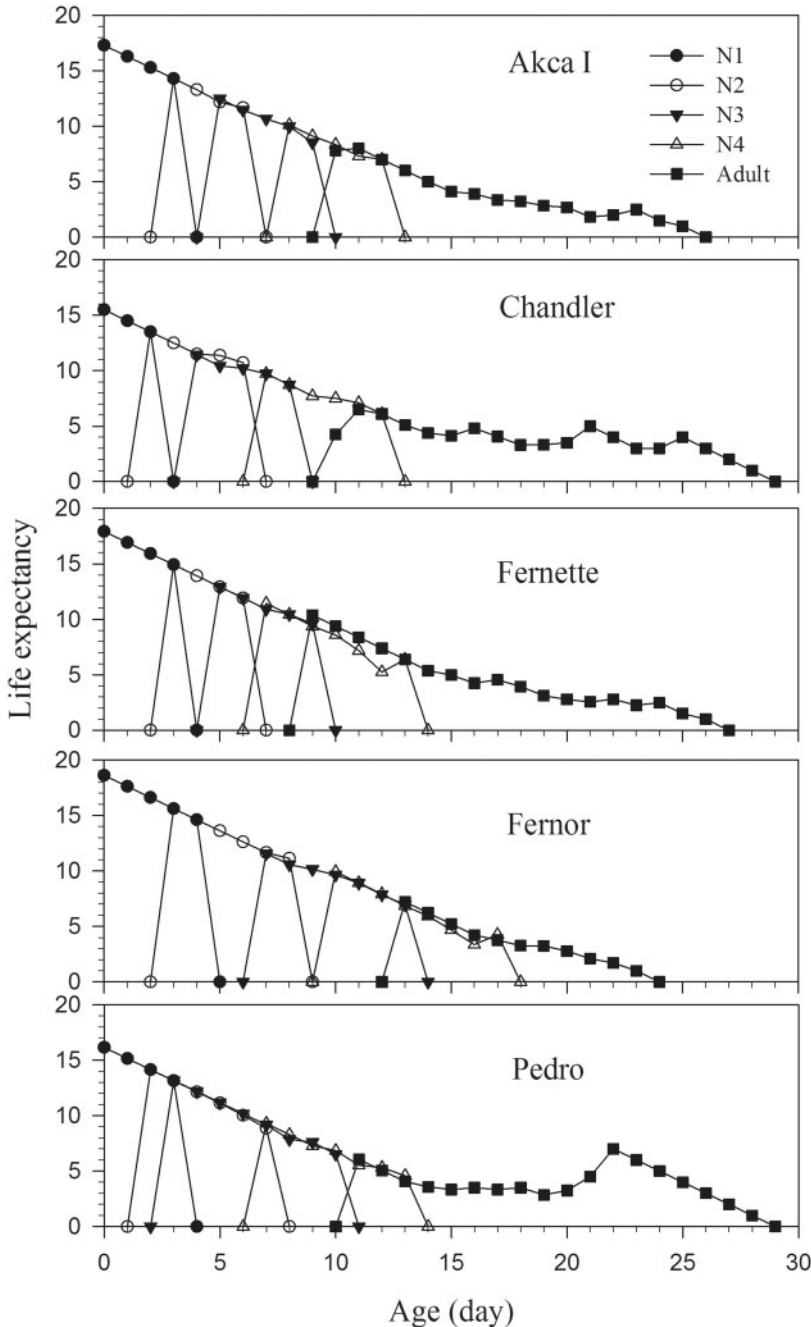
plant sap quality and the proportions of essential nutrients (van Emden 1966, Dodd and van Emden 1979, Kainulainen et al. 2002). Thus, analysis of the sap composition of the walnut cultivars will help to clarify the factors affecting the population growth of

*P. juglandis* on different walnut cultivars. However, adverse effects of the densities of glandular and non-glandular trichomes on aphids have been reported (Greer and Nielsen 1988, Severson et al. 1992). Thurston et al. (1966) and Thurston (1970) demonstrated

**Table 3. Population parameters ( $r$ , intrinsic rate of increase;  $\lambda$ , finite rate of increase;  $R_0$ , net reproductive rate, offspring/individual; and  $T$ , mean generation time) of *P. juglandis* reared on different walnut cultivars (mean  $\pm$  SE)**

Cultivar	$r$ ( $d^{-1}$ )	$\lambda$ ( $d^{-1}$ )	$R_0$ (offspring/individual)	$T$ (d)
Akça I	0.2031 $\pm$ 0.0063a	1.2252 $\pm$ 0.0077a	18.0 $\pm$ 1.5a	14.2 $\pm$ 0.1b
Chandler	0.1854 $\pm$ 0.0097b	1.2038 $\pm$ 0.0117b	15.0 $\pm$ 2.1b	14.5 $\pm$ 0.2b
Fernette	0.1510 $\pm$ 0.0086c	1.1630 $\pm$ 0.0099c	9.4 $\pm$ 1.2c	14.8 $\pm$ 0.2b
Fernor	0.0983 $\pm$ 0.0090d	1.1034 $\pm$ 0.0099d	5.9 $\pm$ 0.9d	17.9 $\pm$ 0.4a
Pedro	0.1666 $\pm$ 0.0087c	1.1813 $\pm$ 0.0102c	11.3 $\pm$ 1.5c	14.5 $\pm$ 0.2b

The standard errors were calculated using the bootstrap procedure with 40,000 bootstraps. The means followed by different letters in the same column are significantly different between cultivars using the paired bootstrap test at 5% significance level.



**Fig. 4.** Age-stage-specific life expectancy ( $e_{xy}$ ) of *P. juglandis* reared on five walnut cultivars.

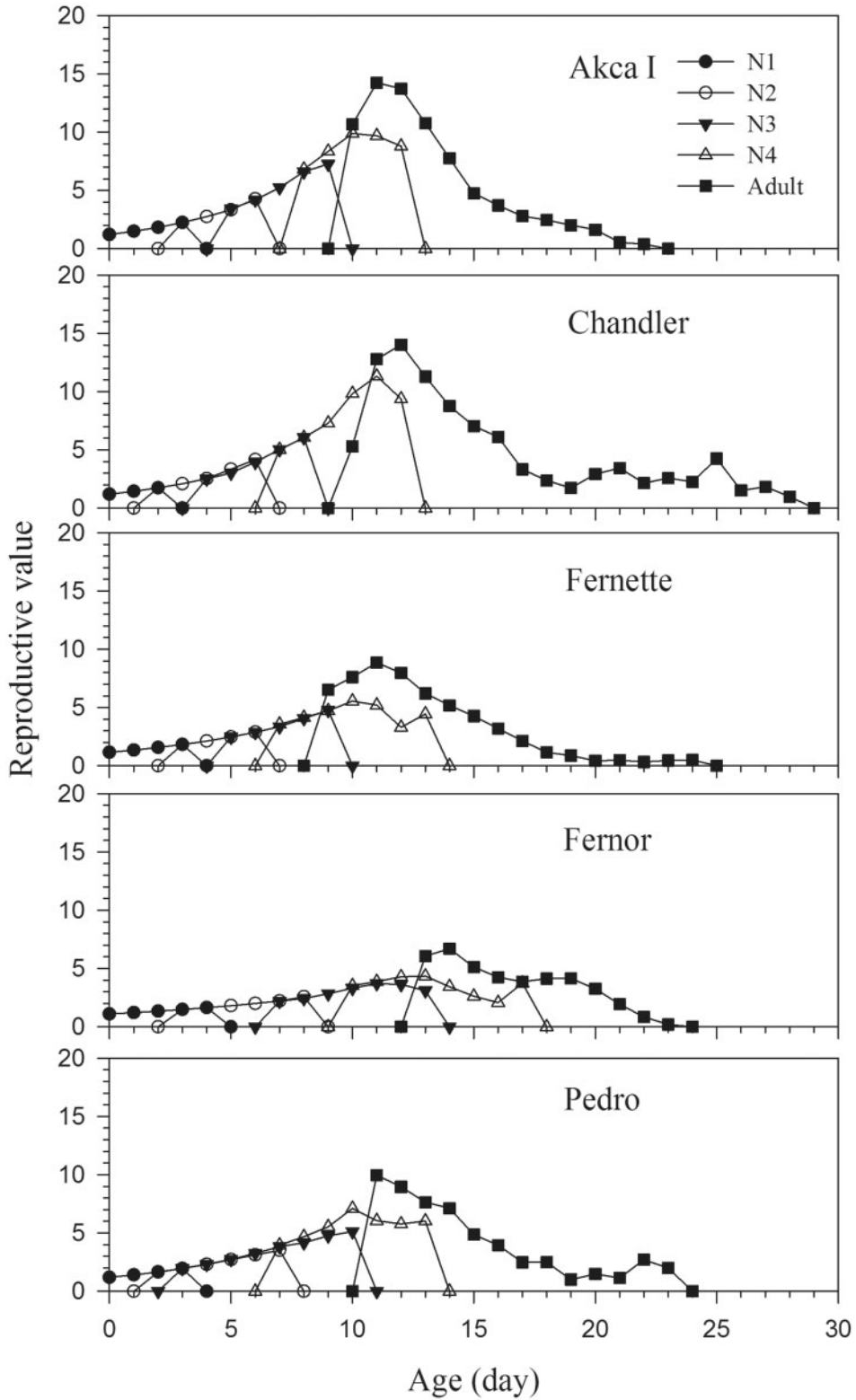


Fig. 5. Age-stage-specific reproductive value ( $v_{xj}$ ) of *P. juglandis* reared on five walnut cultivars.



that glandular trichomes produce alkaloids, diterpenes, and sugar esters, which are highly effective against insects, including aphids. The trichome density of walnut leaves might also affect the performance of aphids.

The intrinsic rate of increase ( $r$ ), finite rate of increase ( $\lambda$ ), and net reproductive rate ( $R_0$ ) reflect the conclusive effect of the development, survival, and reproduction on the population fitness. Among the five walnut cultivars, *P. juglandis* reared on the cultivar Fernor exhibited the lowest intrinsic rate, finite rate, and net reproductive rate. The slower developmental rate, lower daily fecundity, and later peak in reproduction conclusively resulted in the lower population parameters on Fernor. Even a small reduction in these parameters can cause considerable changes in the population sizes of the pests (Goundoudaki et al. 2003). The effectiveness of natural enemies for controlling *P. juglandis* populations on walnut trees might increase with reductions in aphid populations caused by resistant or less-favorable cultivars. However, this hypothesis must be confirmed by studies under field conditions (Goundoudaki et al. 2003).

In this study, worldwide and well-known cultivars were used, except Akça I, which is a new cultivar and is currently only used in Turkey. There are studies showing that some cultivars of the same plants in orchard ecosystems might be less-favorable hosts than other ones (Tang et al. 1999, Özgökçe and Atlıhan 2005). The overall effect of the resistance shown by Fernor can be depicted using population projections based on a life table. The projected growth showed a slower increase in the pest population, which offers more chance for effective biological control and other management strategies. According to our results, Fernor creates a less-favorable environment for aphid development and reproduction. Slower development and population growth on Fernor may allow walnut trees more opportunity to compensate for the damage caused by aphid and reduce the application of insecticides. Our findings are useful for the construction of an IPM program for the control of *P. juglandis* on walnut plants.

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