Eur. J. Entomol. **112**(3): 453–459, 2015
doi: 10.14411/eje.2015.053
ISSN 1210-5759 (print), 1802-8829 (online)

Demographic parameters of *Diuraphis noxia* (Hemiptera: Aphididae) and *Hippodamia variegata* (Coleoptera: Coccinellidae) recorded in the context of *D. noxia* infesting resistant and susceptible cultivars of wheat

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Key words. Hemiptera, Aphididae, *Diuraphis noxia*, Coleoptera, Coccinellidae, *Hippodamia variegata*, Russian wheat aphid, life table, host plant resistance

Abstract. The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a serious pest of small grains and can cause losses of about 80% in wheat yields. Chemical control is ineffective against this pest so the combined use of host plant resistance and biological control is seen as a possible better means of controlling this pest. In this study, the potential effect of Omid (resistant) and Sardari (susceptible) cultivars of wheat on life table parameters and daily fecundity of RWA and its predator, *Hippodamia variegata* (Goeze), were determined using the age-stage two-sex life table theory. The results indicate that the r_m, R_0, λ, T and GRR of RWA were –0.005 ± 0.01 day^{-1}, 0.9 ± 0.24 offspring per individual, 0.99 ± 0.01 day^{-1}, 21.16 ± 1.79 days and 13.34 ± 2.91 offspring on Omid and 0.159 ± 0.01 day^{-1}, 6.9 ± 0.54 offspring per individual, 1.17 ± 0.01 day^{-1}, 12.14 ± 0.26 days and 12.73 ± 1.22 offspring on Sardari. The corresponding values for *H. variegata* fed on RWA reared on Omid were 0.24 ± 0.01 day^{-1}, 399.35 ± 53.01 eggs, 1.27 ± 0.01 day^{-1}, 24.67 ± 0.28 days and 544.23 ± 75.86 eggs and on Sardari 0.20 ± 0.006 day^{-1}, 221.56 ± 34.68 eggs, 1.23 ± 0.01 day^{-1}, 26.50 ± 0.41 days and 402.72 ± 67.55, respectively. The resistance of wheat cultivars significantly affected life table parameters and mean fecundity of RWA and *H. variegata*. Our results indicate that combining both host plant resistance and predators in the integrated pest management of RWA could result in a synergistic effect.

INTRODUCTION

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov) (Hemiptera: Aphididae), is a major pest of small grains, particularly wheat, barley, triticale, rye and wild grasses world-wide and a major cause of economic losses (Farid et al., 1997; Clark & Messina, 1998; Qing Nian et al., 2009; Jimoh et al., 2013). It prefers to feed within the leaf whorl on new leaves (Macedo et al., 2003), injecting a toxin that causes leaf discoloration and distortion. Leaf rolling plays an important role in reducing the effectiveness of certain management strategies, by reducing contact with insecticides and the efficacy of biological control agents (Gutsche et al., 2009). When abundant, RWA reduces wheat yield directly (Kindler & Hammon, 1996). Although a poor vector of plant pathogenic viruses, including barley yellow dwarf virus, barley brome mosaic and barley stripe mosaic (Damsteegt et al., 1992), it nevertheless can reduce the yield of wheat by up to 80% (Hughes & Maywald, 1990).

It is difficult to manage RWA because it has a short life cycle and an extremely high reproductive rate (Dogimont et al., 2010). Insecticides are frequently used to suppress RWA populations but in addition to environmental pollution and risk to non-target beneficial insects, aphids can develop resistance to insecticides, which makes their control more difficult (Dogimont et al., 2010). Host plant resistance is one of the environmentally safe tactics widely used to reduce pest populations (Du Toit, 1987). The use of resistant plants may enhance or reduce the ability of natural enemies to control insect pests (Bottrell et al., 1998; Cortesero et al., 2000; Messina & Sorenson, 2001). Resistant plants may affect the efficacy of important natural enemies of *D. noxia* (Reed et al., 1991) by increasing their accessibility to natural enemies (Messina & Sorenson, 2001). Recent evidence indicates that host plant resistance and RWA predators or parasitoids can be effectively used in combination (e.g. Farid et al., 1997, 1998; Messina & Sorenson, 2001).

The variegated lady beetle, *Hippodamia variegata* (Goeze) feeds on many insect pests such as aphids, psyllids, whiteflies and mealybugs (Franzman, 2002). This species is reported as an important natural enemy of at least 12 different species of aphids infesting a diversity of crops (Franzmann, 2002; Kontodimas & Stathas, 2005). *H. variegata* is part of the natural enemy complex of RWA in Iran and plays a major role in reducing the abundance of this aphid. Therefore, understanding the tritrophic ecology of this predator helps to better control RWA in different situations.

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Life table studies are fundamental to population ecology (Chi & Yang, 2003; Zu et al., 2005). They provide a brief description of mortality, survival, development, age structure and fecundity of a cohort of animals (Chi & Yang, 2003; Gabre et al., 2005; Zu et al., 2005; Huang & Chi, 2011). Moreover, life table parameters are one of the best criteria for assessing the effects of different kinds of prey on predator survival and fecundity (Golizadeh & Jafari-Behi, 2012). Tritrophic studies have shown that in many cases, the nutritional quality of host plants affect prey and predator life histories (Bottrell et al., 1998; Wu et al., 2010). Therefore, it is necessary to study the life table of predators fed on prey reared on different host plants. Although many studies have recorded the life tables of different species of lady beetles and aphids, there are few controlled studies on the effect of prey feeding history on the life history parameters of *H. variegata*. Moreover, most studies have used female age-specific life table to analyse the data whereas in this study age-stage two-sex life table is used. The main aim of this paper is to study the effect of resistant and susceptible cultivars of wheat on the life history and demographic parameters of RWA and *H. variegata*.

MATERIAL AND METHODS

Insect and plant rearing

Two wheat cultivars, the resistant Omid and susceptible Sardari (Kazemi et al., 2001; Najafi Mirak et al., 2004; Dolati et al., 2004) were grown in plastic pots in a greenhouse kept at 25 ± 5°C, 55 ± 10% relative humidity and a 12L : 12D photoperiod (Department of Plant Protection, Faculty of Agriculture, Bu-Ali Sina University, Iran). Russian wheat aphids were collected from different parts of Hamedan province in western Iran. Wheat plants infested with *D. noxia* provided sufficient numbers of RWA for the experiments and the colonies were maintained on two cultivars of wheat for at least three generations. *H. variegata* were collected from an alfalfa field (Hamedan, Amzajerd region, 35°1´N, 48°31´E) and fed by aphids reared on either the resistant or susceptible cultivar of wheat for at least three generations before starting the experiment.

Life tables of *D. noxia* and *H. variegata*

To obtain each RWA cohort, five adults were placed in cylindrical clip cages (30 mm diameter) one of which was clipped to each of the leaves of a wheat seedling. After 12 h, all but one individual were removed leaving a single first instar nymph in each cage. Because, many of the RWA nymphs died prematurely on the resistant cultivar, the number of first instar nymphs reared on the resistant and susceptible cultivars was 202 and 100, respectively. Experimental plants were checked daily and nymphal mortality and developmental time were recorded. After reaching the adult stage, reproduction was recorded by removing the newborn nymphs daily. This procedure continued until the adult aphids died.

A similar procedure was used for studying the life table parameters of *H. variegata*. Lady beetle adults were reared separately on either *D. noxia* reared on resistant or susceptible wheat before the start of the experiment. Then, 107 and 113 newly laid eggs were collected from *H. variegata* fed on aphids of resistant and susceptible wheat seedlings, respectively. After hatching, the larvae were provided with either mixed stages of Omid- or Sardari-reared aphids and as soon as they became adult they were sexed and paired randomly in ventilated Petri dishes (9-cm diameter). An excess of aphids was provided to each pair and the number of eggs produced by each pair recorded daily. If one member of a pair (male or female) in each replicate died, the experiment was continued until the death of the last individual. All experiments were conducted under constant conditions (25 ± 1°C, 60 ± 5% R.H. and a 16L : 8D photoperiod).

Data analysis

Raw data were analyzed based on the age-stage, two-sex life table method (Chi & Liu, 1985; Chi, 1988) in the software program TWOSEX-MS Chart (available at http://140.120.197.173/Ecology/prod02.htm) (National Chung Hsing University, Taichung, Taiwan) and at http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey, Champaign-Urbana, IL) (Zu et al., 2005; Atlihan & Chi, 2008). This method differs from traditional female-based life table analysis in including preadult mortality, variation in the developmental rate of adults and the male contribution to the demographic parameters. Moreover, because mean duration or "adult age" is generally used to construct the survival curve, this results in errors in population parameters (Chi & Liu, 1985; Chi, 1988). The age-stage, two-sex life table is widely used in studies on parthenogenic species (He et al., 2013; Hu et al., 2014).

The most important life history parameter, i.e., intrinsic rate of increase (r_m) was calculated using the Euler-Lotka equation (1),

$$\sum_{x=0}^{\infty} l_x m_x e^{-r_m(x+1)} = 1 \qquad (1)$$

where, x is the age of the aphid (days), l_x is the age-specific survival rate and m_x is the age-specific fecundity rate. Based on the age-stage two-sex life table, the values of l_x and m_x are calculated as:

$$l_x = \sum_{j=1}^{k} s_{xj} \qquad (2)$$

$$m_x = \frac{\sum_{j=1}^{k} s_{xj} f_{xj}}{\sum_{j=1}^{k} s_{xj}} \qquad (3)$$

where, k is the number of stages, x = age, j = stage, s_{xj} is the age-stage survival rate (Chi, 1988; Chi & Yang, 2003).

In addition, life expectancy (e_{xj}), mean fecundity (F) of individual of age x and stage y and other parameters such as net reproductive rate (R_0), finite rate of increase (λ), T (mean generation time) and gross reproductive rate (GRR) were also calculated. Because the jackknife method provides incorrect estimates of the standard errors for R_0 (Jha et al., 2012), bootstrap techniques were used to estimate uncertainty (Efron & Tibshirani, 1993). Independent sample t-tests or non-parametric Mann-Whitney U tests

TABLE 1. Population parameters (± SE) of *Diuraphis noxia* reared on Sadari, a susceptible and Omid, a resistant cultivar of wheat.

Parameter (Unit)	Wheat cultivar	
	Sardari	Omid
r_m (day^{-1})	0.159 ± 0.01	–0.005 ± 0.01
R_0 (offspring)	6.9 ± 0.54	0.9 ± 0.24
λ (day $^{-1}$)	1.172 ± 0.01	0.995 ± 0.01
T (day)	12.14 ± 0.26	21.16 ± 1.79
GRR (offspring)	12.73 ± 1.22	13.34 ± 2.91

r_m – intrinsic rate of increase; R_0 – net reproductive rate; λ – finite rate of increase; T – mean generation time; GRR – gross reproductive rate.

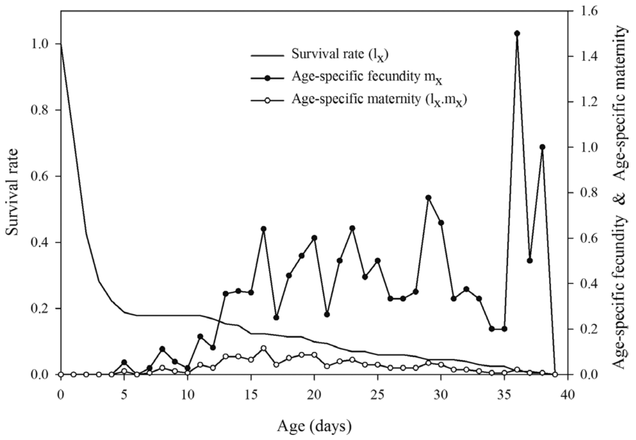

Fig. 1. Trends in time of the age-stage survival rate (l_x), age-specific fecundity (m_x) and maternity ($l_x \cdot m_x$) rate of *Diuraphis noxia* reared on Omid, a resistant cultivar of wheat.

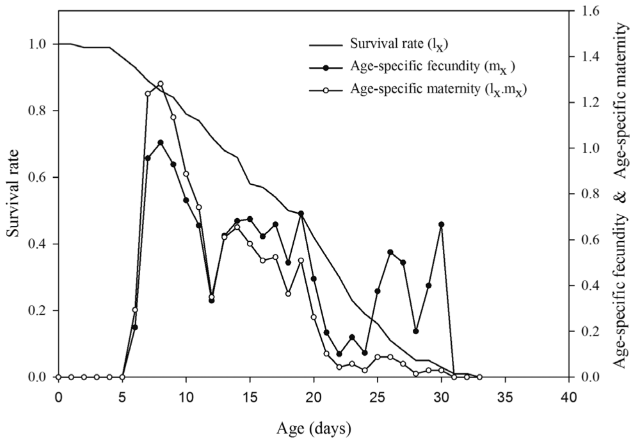

Fig. 2. Trends in the age-stage survival rate (l_x), age-specific fecundity (m_x) and maternity ($l_x \cdot m_x$) rate of *Diuraphis noxia* reared on Sardari, a susceptible cultivar of wheat.

were used to compare life history parameters whenever normality assumptions were not met. In all tests, α was 0.05.

RESULTS

Life history parameters of RWA

Demographic parameters of RWA reared on resistant and susceptible cultivars of wheat are given in Table 1. The differences between the r_m, R_0, λ and T values for RWA reared on Omid and Sardari cultivars of wheat were significant (Mann-Whitney test, U Statistic = 0.000, P-value < 0.001) but not those for GRR (Mann-Whitney test, U Statistic = 491620.00, P-value = 0.516). A decreasing trend in the survival rate of RWA was recorded during the developmental period on both cultivars of wheat, but higher mortalities were recorded on the resistant than on the susceptible cultivar, especially during the early stages of development (Figs 1 and 2). The age-specific fecundity (m_x) indicates that the number of offspring produced by an individual RWA of age *x* on the resistant cultivar reaches its maximum value (1.5) at the end of the reproductive period (day 36), while on the susceptible cultivar the peak (1.024) was recorded three days after the start of reproduction. Because of the low survival rate of RWA on the resistant cultivar the net age-specific maternity, [i.e. the weighted average production of offspring by females aged *x* each day (Carey, 1993)] was very low irrespective of the oscillations in the age-specific fecundity. However, this parameter followed the same trend as m_x recorded on the susceptible cultivar. The female mean fecundity was 7.24 ± 1.38 and 8.02 ± 0.53 on the resistant and susceptible cultivars, respectively.

Stable age distribution of RWA

Table 2 shows the stable age distribution (percentage). It reveals that on both cultivars adults are the most abundant stage followed by first instar nymphs. As the different stages of *D. noxia* have different developmental rates (Fig. 3) there are overlaps in the survival rate curves. This point is ignored in analyses using female-based life tables. In addition, Fig. 3 indicates that the survival rates of all life stages were highest on the susceptible cultivar. Reproductive value, defined as the expected relative contribution of an individual to future population numbers, maximally occurred at an age of 11 days on the resistant and 7 days on the susceptible cultivar.

TABLE 2. Percentage of individuals in each of the developmental stages in populations of *Diuraphis noxia* at stable age distribution on Omid and Sardari cultivars of wheat.

Wheat cultivar	1st instar	2nd instar	3rd instar	4th instar	Adult
Omid	29.98	14. 17	14.32	8.86	32.93
Sardari	27.30	18.22	13.47	8.36	32.46

Population parameters of *H. variegata*

The initial number of lady beetle eggs used in the life table study were 107 and 113 for those reared on aphids collected from susceptible and resistant cultivars of wheat, respectively, of which 90 and 79 reached the adult stage (84% and 69% survival rates, respectively). Life history parameters of *H. variegata* reared on aphids collected from the resistant and susceptible cultivars of wheat are presented in Table 3. Values of r_m (Mann-Whitney test, U Statistic = 0.00, P-value < 0.001), λ (Mann-Whitney test, U Statistic = 0.00, P-value < 0.001), R_0 (Mann-Whitney test, U Statistic = 2682.0, P-value < 0.001), T (Mann-Whitney test, U Statistic = 135.5, P-value < 0.001) and GRR (Mann-Whitney test, U Statistic = 81474.00, P-value < 0.001) differed for ladybirds reared on the resistant and susceptible cultivars of wheat. The trends in age-specific survival curves (l_x), age-specific fecundity (m_x) and age-specific maternity ($l_x \cdot m_x$) of *H. variegata* reared on aphids collected from the resistant and susceptible cultivars of wheat are illustrated in Fig. 4. These figures indicate that *H. variegata* reared

TABLE 3. Population parameters (mean ± SE) of *Hippodamia variegata* fed on *Diuraphis noxia* reared on Sardari, a susceptible and Omid, a resistant cultivar of wheat. Symbols in Table1.

Parameter	Omid	Sardari
r_m (d^{-1})	0.24 ± 0.01	0.20 ± 0.01
R_0 (offspring)	399.35 ± 53.01	221.56 ± 34.68
λ (d^{-1})	1.27 ± 0.01	1.23 ± 0.01
T (day)	24.67 ± 0.28	26.50 ± 0.41
GRR (offspring)	544.23 ± 75.86	402.72 ± 67.55

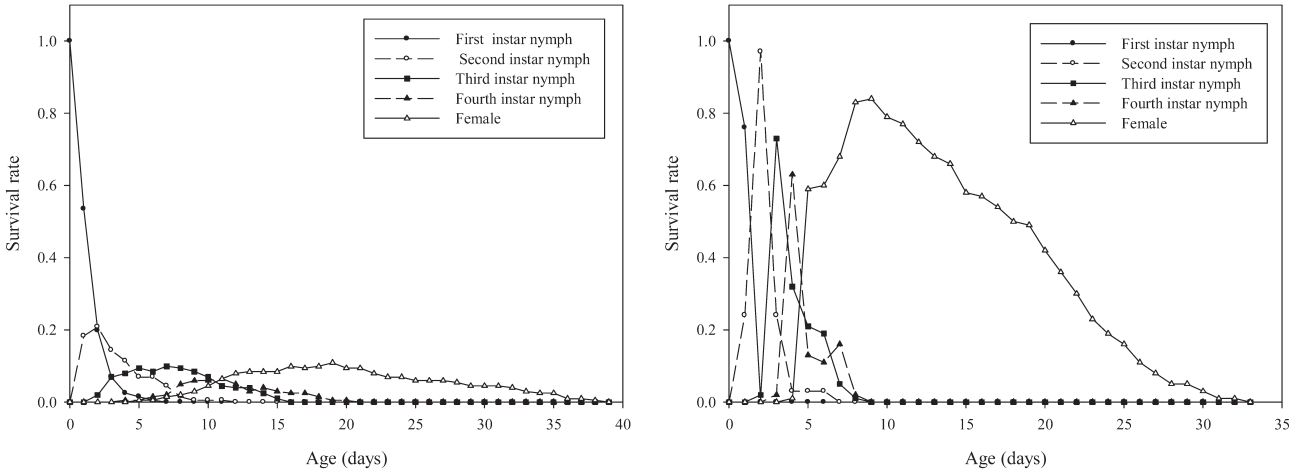

Fig. 3. Survival rate of each age-stage of *D. noxia* reared on the resistant Omid (left) and susceptible Sardari (right) cultivars of wheat.

on aphids collected from the susceptible cultivar of wheat started laying eggs on day 17 and ceased on day 85 (68 days), while those reared on aphids collected from the resistant cultivar of wheat started laying eggs on day 16 and ceased on day 63 (47 days). However, the oscillations in the age-specific fecundity recorded for *H. variegata* fed RWA reared on the resistant cultivar were greater than for those fed RWA reared on the susceptible cultivar (Fig. 4).

Plant resistance affected maximum daily and maximum total fecundity of *H. variegata* with 142 and 125 eggs, and 1716 and 1480 eggs for lady beetles fed *D. noxia* reared on the resistant and susceptible cultivars of wheat, respectively. Maximum reproductive values of *H. variegata* fed *D. noxia* reared on the resistant and susceptible cultivars of wheat were 101.63 and 79.29, which were recorded when they were 18 and 21 days old, respectively. Survival curves of *H. variegata* recorded over the complete developmental period when fed aphids reared on both cultivars of wheat were similar (Fig. 5). The overlapping curves reflect the different developmental rates of the different stages.

Stable age distribution of *H. variegata*

The stable age distributions of *H. variegata* fed RWA reared on both cultivars of wheat are shown in Table 4. The stable age distribution of *H. variegata* in both cases are similar, with more than half of the lady beetle population made up of eggs and third instar larvae the least abundant of the larval stages.

DISCUSSION

This tritrophic study confirmed that the nutritional quality of a host plant affects both the herbivore that feeds on it and its natural enemy. The lower values of life table parameters (r_m, R_0 and λ) recorded for RWA reared on the resistant cultivar of wheat demonstrate the effectiveness of plant resistance against RWA. When reared on the resistant cultivar the intrinsic rate of increase (r_m) of RWA was negative (i.e. the population decreased). This might be due to higher immature mortality or reduced fecundity. The age-stage survival rate (l_x) curve indicates that more than half of the nymphs died before reaching the second instar when reared on the resistant cultivar. In addition, the net reproductive rate (R_0) and the finite rate of increase (λ) of *D. noxia* were similarly dependent on the cultivar of wheat they were reared on. Furthermore, on the resistant wheat cultivar the developmental period and mean generation time (T) of *D. noxia* were longer. This effect has consequences in terms of the temporal availability of aphids for natural enemies.

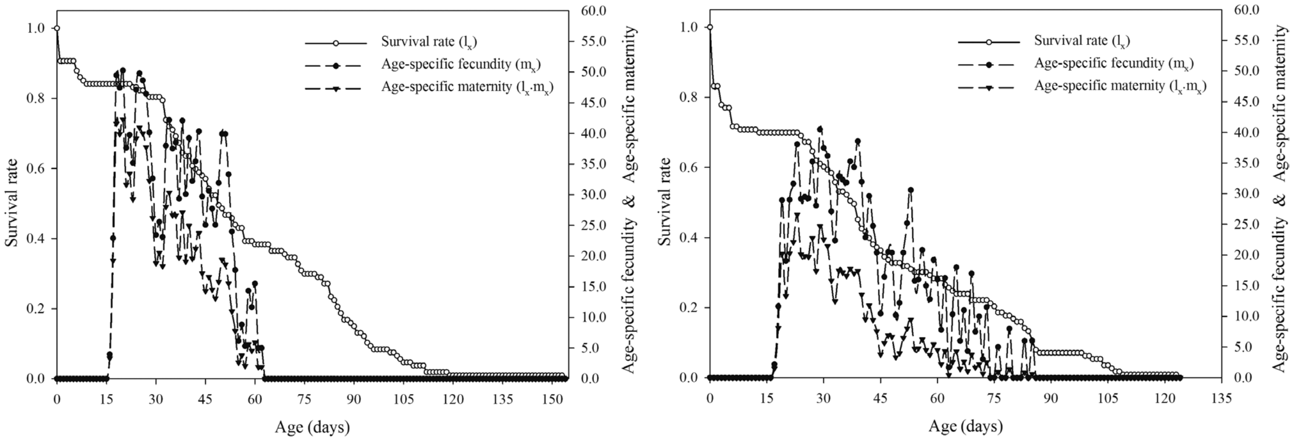

Fig. 4. Trends in the age specific survival (l_x), age-specific fecundity (m_x) and maternity ($l_x \cdot m_x$) of *Hippodamia variegata* fed on Russian wheat aphids reared on Omid (R, left) and Sardari (S, right) cultivars of wheat.

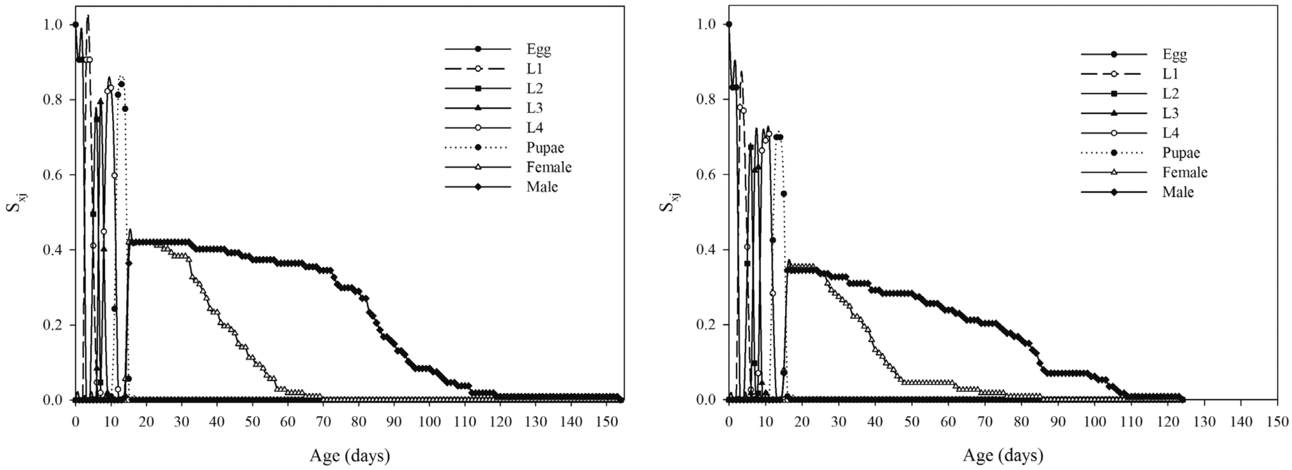

Fig. 5. Survival rate of each age-stage of *Hippodamia variegata* fed on Russian wheat aphids reared on Omid (R, left) and Sardari (S, right) cultivars of wheat.

As developmental time increases, the chances of natural enemies finding and killing an aphid increases.

A study of the resistance of five cultivars of wheat: Alamoot, Alvand, Zarrin, Sabalan and Sardari, to RWA under field conditions in Tabriz, northwest of Iran, indicates that the greatest and the lowest numbers of progeny produced / female over the first 10 and 15 days of reproduction, respectively, are 34.94 ± 5.91 and 48.56 ± 7.66 on Sardari and 24.83 ± 9.36 and 36.67 ± 13.67 on Alvand (Kazemi et al., 2001). Moreover, the highest r_m values recorded within 10 and 15 days were 0.268 ± 0.02 day^{-1} and 0.264 ± 0.02 day^{-1}, respectively for individuals reared on Sardari and the lowest, 0.217 ± 0.03 day^{-1} and 0.223 ± 0.03 day^{-1} on Alvand. Effects of different temperatures and different barley plant growth stages on life table parameters of RWA are reported by Ma & Bechinski (2009) who record the highest intrinsic rate of increase as 0.288 day^{-1} at 25.08°C on stage 12 (Zadoks scale). Veisi et al. (2012) record total fecundities of 61.75 ± 7.93 and 24.00 ± 0.81, and mean offspring produced per female per day of 2.51 ± 0.43 and 1.40 ± 0.19 on the cultivars Yavarus and Omid, respectively. Overall, they conclude that Yavarus is susceptible and Omid resistant to RWA.

The most striking finding of our study is that plant quality positively affects the life history parameters of *H. variegata*. Based on the r_m and other demographic parameters of *H. variegata*, the resistance of wheat to *D. noxia* did not negatively affect the growth, survival and fecundity, and improved the population growth of *H. variegata*. That is, *H. variegata* grew faster and laid more eggs when feed on RWA reared on a resistant than on an aphid-susceptible cultivar of wheat. This dual effect of host plant resistance may be of chemical origin. Natural secondary plant metabolites of the resistant cultivar might have had adverse effects on RWA but when metabolized by the aphid have a positive effect on the reproduction and survival of *H. variegata* relative to that recorded when fed the aphid reared on a susceptible cultivar that lacks these metabolites (Barkhordar et al., 2013). In addition, it is possible these differences are a consequence of differences for *H. variegata* in the digestibility of RWA reared on resistant and susceptible cultivars (Barkhordar et al., 2013).

Table 4. Stable age distributions (%) of populations of *Hippodamia variegata* fed on aphids reared on Sadari, a susceptible and Omid, a resistant cultivar of wheat.

Cultivar	Egg	L_1	L_2	L_3	L_4	Pupae	Female	Male
Omid	53.48	21.55	7.78	5.30	6.53	2.95	1.24	1.18
Sardari	50.69	20.90	8.08	6.42	7.04	3.47	1.70	1.69

The life history of *H. variegata* reared at different temperatures and on different diets is well studied. Differences are reported in the demographic parameters of *H. variegata* fed on different species of aphids. El Hag & Zaitoon (1996) compare four species of coccinellids in terms of their biological parameters and report an r_m value of 0.082 day^{-1} for *H. variegata*. Mollashahi et al. (2004) studied population growth parameters of *H. variegata* fed on *Aphis gossypii* Glover and report that the intrinsic rate of increase (r_m) and net reproductive rate (R_0) of this predator are 0.254 day^{-1} and 387.9 eggs, respectively. Lanzoni et al. (2004) report an intrinsic rate of increase of 0.114 day^{-1} for *H. variegata*, which is higher than that of *Harmonia axyridis* (Pallas) and *Adalia bipunctata* (L.) fed on *Myzus persicae* (Sulzer). Farhadi et al. (2011) report an r_m value of 0.203 ± 0.005 day^{-1} for *H. variegata* fed bean aphids, *Aphis fabae* Scopoli, which is similar to the value recorded in this study for *H. variegata* fed on RWA reared on the susceptible cultivar of wheat. In addition, parameters other than R_0 have similar values. The r_m of *H. variegata* fed on *A. gossypii* is 0.179 ± 0.005 day^{-1} (Bigdelou, 2012).

Our results indicate that not only the type of prey but also the quality of the host plant of the prey can have substantial indirect effects on the life table parameters and effectiveness of ladybirds. This is also reported for other predator-prey systems (Ofuya, 1995; Wu et al., 2010). Farid et al. (1997) report that the percentage mortality of *Scymnus frontalis* (Fabricius, 1787) (Coleoptera: Coccinellidae) larvae is higher on susceptible than on RWA-resistant plants and attribute this to the greater incidence of entrapment of *D. noxia* by curled leaves of susceptible cultivars of wheat.

Cultivar resistance did not affect the weight of the larvae, prepupae, pupae and adults or the total developmental time of *S. frontalis*. Different results are reported by Brewer et al. (1998) who show that use of barley resistant to RWA results in a decrease in the abundance of *Diaeretiella rapae* (Mc Intosh) and *Aphelinus albipodus* Hayat & Fatima as aphid abundance decreases, even though parasitism rates were expected to be approximately equal on resistant and susceptible barley. Farid et al. (1998) report that although the rate of population increase of *D. noxia* is lower on a resistant cultivar of wheat over a period of three generations, plant resistance did not have a negative effect on percentage emergence, sex ratio, adult longevity, or head width of *D. rapae*. Furthermore, when parasitoids emerge from aphids reared on resistant cultivars the longevity of females is greater. Thus, host plant resistance can affect both growth and development of *D. rapae*. The abundance of *D. noxia* on resistant barley lines is lower than on more susceptible lines (Brewer et al., 1998). In addition, the abundance of the parasitoids *D. rapae*, *A. albipodus* and *Aphelinus asychis* Walker, 1839 on resistant and susceptible barley lines is similar (Brewer et al., 1999). They also conclude that in this system, the use of plant resistance and natural enemies are compatible strategies.

The larvae of the lacewing *Chrysoperla plorabunda* (Fitch) cause a greater proportional reduction in the abundance of RWA on resistant than on near isogenic susceptible lines of wheat, which indicates that lacewings are more effective on resistant plants (Messina & Sorenson, 2001). The smaller aphid populations or smaller size of individual prey on resistant cultivars may in this case be the cause of the increase in predator effectiveness (Messina & Sorenson, 2001). Only the larvae of lacewings prey on aphids and therefore they are less exposed to the defensive chemicals of resistant plants. In spring wheat fields in Moscow, Idaho there is no interaction between plant resistance and the population densities of predators and parasitoids (Bosque-Perez et al., 2002). Thus, *D. noxia* resistant lines do not have any adverse effects on the natural enemies (parasitoids and predators) of *D. noxia*. However, other studies have demonstrated negative effects of Bt-crops and resistant varieties on parasitoid and predator biology and fecundity (Schuler et al., 1999).

The current study highlights the effect of plant resistance on the 3rd trophic level. If the positive effect of resistant cultivars on *H. variegata* is shown to occur in the field then the release of a fixed number of *H. variegata* should decrease prey abundance even in the lower populations recorded on resistant cultivars (Messina & Sorenson, 2001). These results increase our understanding of the effects of host resistance on natural enemy biology and if relevant to field conditions, the possibility of important interactions in IPM programs. A biocontrol agent, especially a parasitoid would be more effective if it had a higher r_m than its host. In the present study, the ladybird beetles reared on two different types of prey had higher rates of increase than RWA, which indicates that *H. variegata* is a suitable candidate for release against RWA, especially on resistant cultivars of wheat. It is probable that application of this predator on a resistant cultivar might lead to a greater synergistic effect in RWA population. However, it is unclear if this effect is chemically mediated and if so, what the biochemical basis for it is.

ACKNOWLEDGEMENTS. We are grateful to M. Sameni and T. Behnazar for their cooperation. Special thanks to F. Shirzadi for editing an early draft of the manuscript. This study was funded by the Faculty of Agriculture, Bu-Ali Sina University, Hamedan, Iran and formed a part of the M.Sc. thesis of the first author.

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Received June 16, 2014; revised and accepted February 12, 2015