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Research

Comparison of Life Table Parameters and Digestive Physiology of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) Fed on Various Barley Cultivars

Maryam Nemati-Kalkhoran, Jabraeil Razmjou,[1] Ehsan Borzoui, and Bahram Naseri

Department of Plant Protection, Faculty of Agriculture and Natural Resources, University of Mohaghegh Ardabili, Ardabil, Iran and [1]Corresponding author, e-mail: razmjou@uma.ac.ir

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Abstract

In this study, the effect of 20 barley cultivars were evaluated on the life table parameters and digestive enzymatic activity of the lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) under laboratory conditions (28 ± 1°C, 60 ± 5% RH, and a photoperiod of 16:8 (L:D) h). Among barley cultivars tested developmental time of *R. dominica* immature stages was longest on cultivar Bahman (61.00) and shortest on Mahoor (46.60 d). The lowest realized fecundities were recorded for insects reared on cultivar Bahman (217.60); and the highest ones were observed for insects reared on Sahra (348.05 eggs/female). The net reproductive rate (R_0) was significantly affected by various barley cultivars being lowest on cultivar Bahman (53.98) and highest on Mahoor (146.79 offspring/female). Records for intrinsic rates of increase (r_m) were lowest on cultivar Dasht (0.043) and the highest on Mahoor (0.066 day^{-1}). The highest levels of amylolytic and proteolytic activity were recorded on cultivars Mahoor and EBYT-92-10, respectively. By contrast, the insects reared on cultivars Dasht had the lowest levels of α-amylase and general protease activity. Correlation analyses showed that high correlations existed between the immature period, adult longevity, fecundity, and life table parameters on one side and protein content and particle size index on the other. The results of our experiments showed that cultivar Mahoor was a relatively susceptible and cultivars Bahman and Dasht were relatively resistant to *R. dominica* which could be useful in the development of IPM programs for this pest in store.

Key words: lesser grain borer, life table, survival rate, fecundity, digestive physiology

Cereal grains, such as barley (*Hordeum vulgare* L.), are the most important source of dietary carbohydrate and protein for humans globally (McKevith 2004). The lesser grain borer, *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae), is one of the major pests of stored grains in many regions of the world (Edde 2012). This pest feeds in grains both as a larva and as an adult. Damaged seeds lose weight and market value and they are generally unacceptable for human consumption (Watts and Dunkel 2003, Astuti et al. 2013). Detection of the insects is difficult because larvae and adults tend to remain hidden inside the seeds (Fargo et al. 1989, Vela-Coiffier et al. 1997).

Postharvest loss to insect pests, such as *R. dominica*, is a serious problem for agriculture (Cuperus and Krischik 1995). Synthetic chemical insecticides have proved very effective in the control of the beetle in store. However, being an internal feeder, it is very difficult to control the larval stage of *R. dominica* with insecticides. Also, the use of insecticides increases production costs and usually results in target insects resistance (Boeke 2002, Collins 2006) as well as leads to environmental and consumer health risks (Hagstrum and Subramanyam 1996). Therefore, there is a need for the ecologically benign methods to control *R. dominica* on grains.

It has previously been suggested that an integrated pest management strategy to protect grains in storage systems could be performed utilizing resistant cultivars (Rossa et al. 2013, Hosseininejad and Naseri 2015, Golizadeh and Abedi 2017, Majd-Marani et al. 2017). However, there is a little published information that has examined the management of *R. dominica* by resistant cultivars. Toews et al. (2000) studied the resistance of eight U.S. wheat cultivars to *R. dominica*, and reported that cultivar Newana was the most resistant to this pest. Also, Chougourou et al. (2013) studied the susceptibility of some rice varieties to the lesser grain borer and reported that the lowest growth of *R. dominica* population was on cultivar WAB56-104. Toews et al. (2001) found that physical and chemical parameters of seeds can strongly influence the progeny of *R. dominica* on wheat cultivars. Edde (2012) reviewed the life table parameters of *R. dominica* at different temperatures and noted

that range 29 to 34°C were more suitable for the development of this pest.

There is evidence that insects regulate intake of multiple nutrients simultaneously and, instead of maximizing intake, avoid ingesting deficits or surpluses relative to regulated points (Raubenheimer and Simpson 2004, Deans et al. 2015). In contrast, when the insects are restricted to imbalanced foods, they employ regulatory factors such as digestive enzymes that govern the extent to which nutrients occurring in deficits or surpluses are eaten (Patankar et al. 2001, Borzoui et al. 2017).

The two major groups of digestive enzymes are α-amylases and proteases, which are synthesized in the insect midgut and play an important role in the intermediary digestion of carbohydrates and proteins, respectively. Different grain cultivars and genetically modified cereals can, e.g., contain compounds such as the proteinaceous inhibitors of amylolytic or proteolytic enzymes that may increase resistance to insect pests by hampering their development (Piasecka-Kwiatkowska and Warchalewski 2000a,b).

There are no published data concerning the life table parameters and dietary responses of *R. dominica* on various barley cultivars, as the main host of this pest in Iran. Therefore, two main goals of this research are: 1) to study the biological and life table parameters of *R. dominica* on various barley cultivars and 2) to determine how the physico-chemical characteristics of tested cultivars affected digestive physiology, and following life table parameters of this coleopteran pest. We expected that high quality of seeds, in terms of macronutrients, hardness, and size, would improve life table parameters, followed by a better regulation in the activity of enzymes, based on the previous studies showing such a link.

Materials and Methods

Barley Sources

Twelve cultivars of barley (*Hordeum vulgare* L.) including Bahman, Dasht, Mahoor, Sahra, EBYT-92-2, EBYT-92–4, EBYT-92–5, EBYT-92–6, EBYT-92–7, EBYT-92–8, EBYT-92-10, EBYT-92-11, which are commercially important in Iran, were obtained from Research Institute of Agriculture and Natural Resources Ardabil (Ardabil, Iran). Cultivars represented divergent genetic lineages. To eliminate the possibility of existing infestations, samples were maintained at –20°C for 3 d. Grains were then kept at –70°C for 12 h and subsequently maintained at 60°C for 12 h. The moisture content of the barley cultivars was adjusted to 14 ± 0.5% by adding water or by ambient drying and then used for the experiments.

Starch Determination

The iodine reagent method was used to assay starch content of tested barley cultivars (Borzoui et al. 2015). Starch content was quantified according to the method of Bernfeld (1955) using starch. This experiment was replicated five times.

Protein Determination

The protein content of the tested barley cultivars was measured using bovine serum albumin (Bradford 1976).

Seed Hardness Determination

The experimental barley hardness was determined by standard particle size index (%) method (AACC 55-30 2000). One thousand and five hundred seeds in five replications (each replication included 300 seeds) were randomly collected and carried out for each cultivar.

One Hundred-Seed Weight Determination

The weight of seeds of tested barley cultivars was determined as the mean hundred-seed weight (Fouad et al. 2013). Five hundred seeds in five replications (each replication included 100 seeds) were randomly collected and weighed using an electronic balance.

Insect Colony

Rhyzopertha dominica beetles were reared on whole barley kernels of each cultivar at 28 ± 1°C, 60 ± 5% RH, and a photoperiod of 16:8 (L:D) h at the Laboratory of Entomology, University of Mohaghegh Ardabili. The rearing was started in 2015 from insects collected from stored wheat seeds from Ardabil, Iran. The *R. dominica* tested on various barley cultivars had already been reared for two generations on the same cultivars. After colonization, male and female adults were transferred to plastic tubes (diameter 2 cm, height 5 cm) containing fine-sifted flour and allowed to oviposit. The deposited eggs (within 24 h) were used for experiments.

Experiments

Life table experiments were started by picking up the eggs (within 24 h) with a fine paint brush, and keeping single eggs in individual Petri dishes (diameter 6 cm, depth 1 cm), containing one seed of each cultivar (Borzoui et al. 2015). The Petri dishes were then checked daily, and the duration of immature stages (egg stage and larval and pupal stages), immature survival and adult longevity were recorded. After eclosion, newly emerged beetles were sexed based on their genital lobe morphology and transferred to the plastic tubes (one male and one female) containing fine-sifted flour of each cultivar. The number of adults coupled for each cultivar depended on survival from the previous stage and ranged from 15 to 26 pairs. Daily adults were transferred to the new tubes with food provided. The number of eggs laid by each female was counted daily. All eggs collected in this study were maintained for 20 d to determine the percentage of hatched eggs (fertility).

The development times, the survival rate of immature stages, and fecundity were used for calculation of life table parameters. Calculations were made for age-specific survival rate (l_x), age-specific fecundity (m_x) of *R. dominica* on twelve barley cultivars according to the method cited in Chi and Su (2006). Estimates were made for the intrinsic rate of natural increase (r_m) for *R. dominica* on various barley cultivars Huang and Chi (2013). Net reproductive rate (R_0), gross reproductive rate (*GRR*), finite rate of increase (λ), and mean generation time (*T*) was also calculated based on Huang and Chi (2013).

Preparation of Sample and Enzyme Assays

Gut extracts of *R. dominica* reared on various barley cultivars were obtained by a slight modification of the method described by Borzoui and Bandani (2013). For each sample, 50 guts were homogenized in 1.0 ml of water by using a precooled homogenizer (Teflon pestle). The homogenates were centrifuged at 15,000 *g* for 15 min at 4°C. The supernatant was recovered and stored at –20°C until used as an enzyme source for subsequent use.

For the determination of α-amylase activity (Bernfeld 1955), 20 µl of the homogenates were added to 40 µl 1% soluble starch + 500 µl MES buffer (2-(*N*-morpholino)ethanesulfonic acid) (50 mM, pH 6.0) and incubated for 30 min at 37°C. To this mixture, 400 ml dinitrosalicylic acid Reagent (DNS) was added, heated in boiling water for 10 min and cooled to room temperature for 5 min. The absorbance was measured at 540 nm after cooling on ice. This experiment was replicated five times for each diet.

Proteolytic activity was carried out as described by Elpidina et al. (2001) with slight modifications using 1.5% (w/v) azocasein as a substrate. For this purpose, 80 µl of azocasein prepared in MES buffer (50 mM, pH 5.5) incubated with 50 µl of gut enzyme extract for 30 min at 37°C. After incubation, the reaction was terminated by the addition of 100 ml of 30% trichloroacetic acid (TCA), continued by cooling at 4°C for 30 min and centrifuging at 15,000 *g* for 10 min. After centrifugation, 100 µl of the supernatant was added to equal volume of NaOH (2 M) and the absorbance was measured at 440 nm. This experiment was replicated five times for each diet.

Statistical Analysis

Before analysis, all the data were examined for normality using Kolmogorov-Smirnov test (PROC GLM; SAS Institute 2011). Since the data were normally distributed, no data transformation was conducted. Results are given as mean ± SD. The bootstrap method was used to estimate the means, variances, and standard errors of the population parameters (Efron and Tibshirani 1993). Also, developmental and enzymatic activity data were compared by ANOVA. Differences between treatment means were evaluated using Turkey's test. The acceptance level of statistical significance was $P < 0.05$. The Pearson correlation coefficient was used to examine the relationships between life table parameters and digestive enzymatic activity of *R. dominica* with physico-chemical traits of tested seeds using SPSS 16.0.

Results

Development Period and Adult Longevity

The results of the effect of various barley cultivars on the developmental time of *R. dominica* are given in Table 1. There were significant differences in the mean incubation period among the barley cultivars ($F_{11,610} = 49.32$; $P < 0.001$). The longest incubation period was on cultivar Bahman, while the shortest one was on Sahra and Mahoor. There was a statistical difference in the development period of larvae and pupae ($F_{11,465} = 47.61$; $P < 0.001$) between the 12 barley cultivars, that was longest when *R. dominica* was fed on cultivar Bahman. The total development period from egg to adult emergence was the longest on cultivars Bahman and EBYT-92-6, and the shortest on Mahoor and Sahra ($F_{11,465} = 71.53$; $P < 0.05$) (Table 1).

Various barley cultivars showed a significant effect on adults longevity of *R. dominica* ($F_{11,227} = 67.69$; $P < 0.001$ for male; $F_{11,226} = 65.53$; $P < 0.05$ for female) (Table 1). Records for shortest and longest longevity of *R. dominica* male were for cultivars EBYT-92-11 and Mahoor, respectively. The record for longevity of *R. dominica* female was the shortest on cultivar EBYT-92-6 and longest on Bahman.

Survival Rate and Fecundity

Figure 1 indicates the age-stage specific survival rate (s_{xj}) of *R. dominica* when reared on various barley cultivars. According to the obtained results, the age-stage survival rate recorded at the larval and pupal stages was highest on cultivar Mahoor and lowest on Dasht. In addition, both male and female adults were short-lived on cultivar Dasht and s_{xj} curve was less extended on this cultivar.

The age-specific number of progeny per day (m_x) of *R. dominica* for various barley cultivars are presented in Fig. 2. The value of m_x was highest on cultivar EBYT-92-10 at an age of 67th day with 10.22 egg/female, and the lowest on Dasht with 6.42 egg/female on the 81st day.

Oviposition Period, Fecundity and Fertility

The pre-oviposition and oviposition periods of *R. dominica* females on the 12 barley cultivars are shown in Table 2. The longest pre-oviposition period ($F_{11,226} = 64.54$; $P < 0.001$) was recorded for cultivar EBYT-92-4, and the shortest was on EBYT-92-6, EBYT-92-5 and Mahoor. In addition, the oviposition period ($F_{11,226} = 52.13$; $P < 0.001$) was longest on cultivars EBYT-92-6 and Mahoor, and shortest on Bahman (Table 2).

The total fecundity of *R. dominica* females significantly differed among the barley cultivars tested ($F_{11,226} = 52.13$; $P < 0.001$). The lowest fecundity was recorded for females developed from larvae fed on cultivars Bahman and Dasht, while the highest fecundity was recorded for females developed from larvae fed on Sahra (Table 2).

Population Growth Parameters

The net reproductive rate (R_0), gross reproductive rate (GRR), intrinsic rate of increase (r_m), finite rate of increase (λ) and mean generation time (T) of *R. dominica* on cultivar Mahoor were 146.79 offspring, 176.40 offspring, 0.066 d^{-1}, and 1.069 d^{-1} respectively, all significantly higher than the values

Table 1. Mean (±SE) duration (days) of immature stages and longevity of *Rhyzopertha dominica* fed on various barley cultivars

Barley cultivars	Immature period						Adult longevity			
	n[a]	Egg	*n*	Larva and pupa	*n*	Total	*n*	Male	*n*	Female
EBYT-92-2	51	9.92 ± 0.16c	40	41.40 ± 2.55d	40	51.32 ± 2.57de	20	108.20 ± 4.37d	20	94.35 ± 3.74de
EBYT-92–4	51	10.81 ± 0.15ab	33	47.78 ± 1.45ab	33	58.60 ± 1.50ab	17	87.23 ± 4.17e	16	78.56 ± 3.03gh
EBYT-92–5	55	9.06 ± 0.13d	43	40.37 ± 2.59de	43	49.44 ± 2.61ef	22	114.04 ± 2.06bcd	21	100.85 ± 3.38cd
EBYT-92–6	56	8.84 ± 0.14de	45	39.42 ± 1.49de	46	48.34 ± 1.54h	23	115.50 ± 1.37bcd	23	112.21 ± 3.34a
EBYT-92–7	54	10.21 ± 0.16bc	46	43.69 ± 1.53cd	46	53.91 ± 1.53ef	23	111.30 ± 3.62cd	23	96.78 ± 3.07cd
EBYT-92–8	53	10.72 ± 0.17abc	36	44.55 ± 1.40c	36	55.27 ± 1.49cd	16	90.75 ± 1.28e	20	88.45 ± 2.87ef
EBYT-92-10	52	9.02 ± 0.14de	42	40.33 ± 1.59de	42	49.35 ± 1.59gh	22	118.81 ± 2.28abc	20	110.65 ± 4.31ab
EBYT-92-11	50	10.71 ± 0.16abc	35	46.34 ± 2.70bc	35	57.05 ± 2.70bc	16	81.06 ± 3.03e	19	84.10 ± 3.18fg
Bahman	42	11.31 ± 0.13a	29	49.68 ± 1.62a	29	61.00 ± 1.56a	14	84.71 ± 4.30e	15	69.80 ± 2.95h
Dasht	50	11.03 ± 0.15ab	31	47.80 ± 2.84ab	31	58.83 ± 2.86bc	16	87.43 ± 4.36e	15	81.33 ± 3.35fg
Mahoor	56	8.42 ± 0.13e	50	38.14 ± 0.84e	50	46.60 ± 0.87fg	24	126.79 ± 3.53a	26	102.92 ± 1.92bc
Sahra	54	8.46 ± 0.11e	47	39.74 ± 1.42de	47	48.17 ± 1.45fg	27	120.62 ± 3.68ab	20	104.00 ± 4.07bc

The means followed by different letters in the same column are significantly different (Turkey's test, $P < 0.05$).
[a]The *n* value shows the sample size for each parameter.

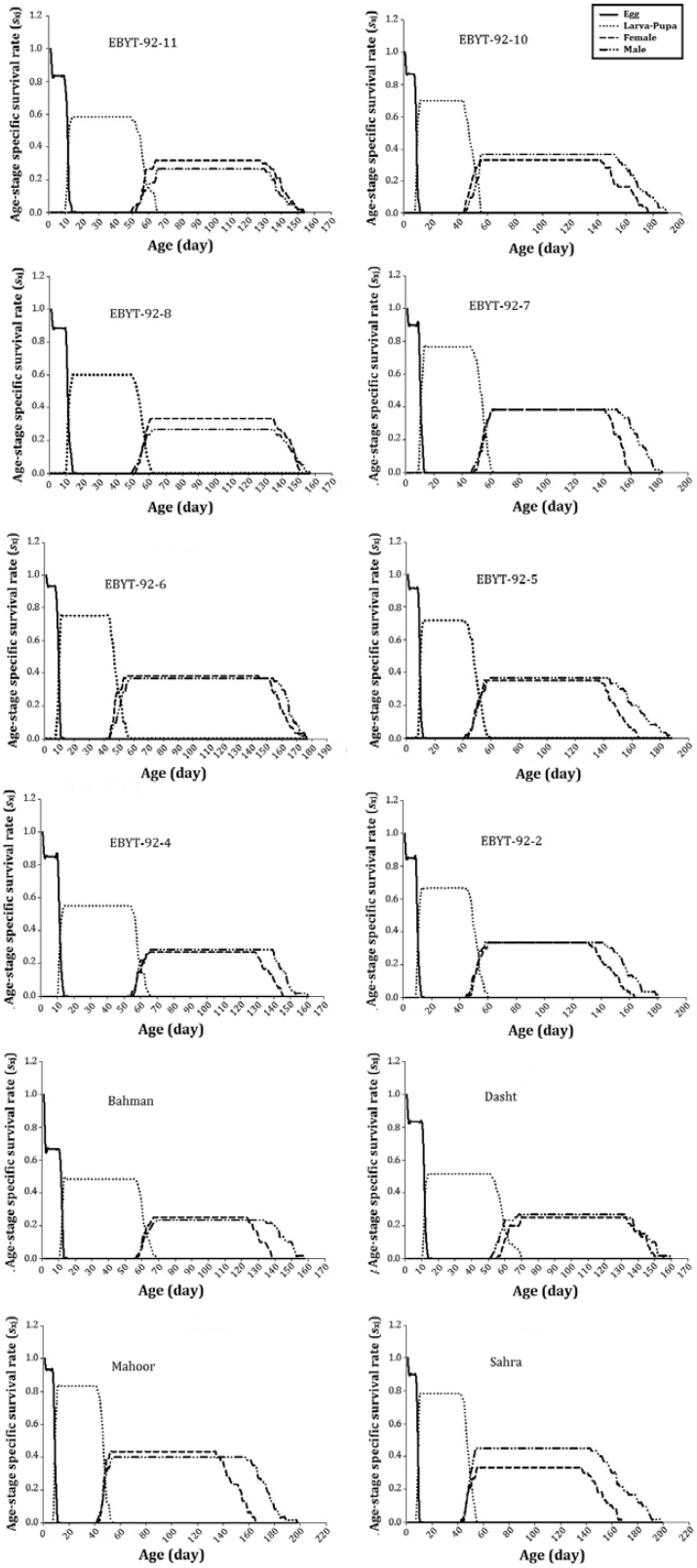

Fig. 1. Age-stage specific survival rate (s_{xj}) of *Rhyzopertha dominica* reared on various barley cultivars.

obtained on other barley cultivars ($F_{11,5988}$ = 1340.51; P < 0.001 for R_0, $F_{11,5988}$ = 441.10; P < 0.001 for GRR, $F_{11,5988}$ = 4175.47; P < 0.001 for r_m, $F_{11,5988}$ = 4180.69; P < 0.001 for λ). On the other hand, the mean generation time (T) obtained on cultivar Mahoor (74.41 d) was shorter than that on other cultivars ($F_{11,5988}$ = 17336.3; P < 0.001) (Table 3).

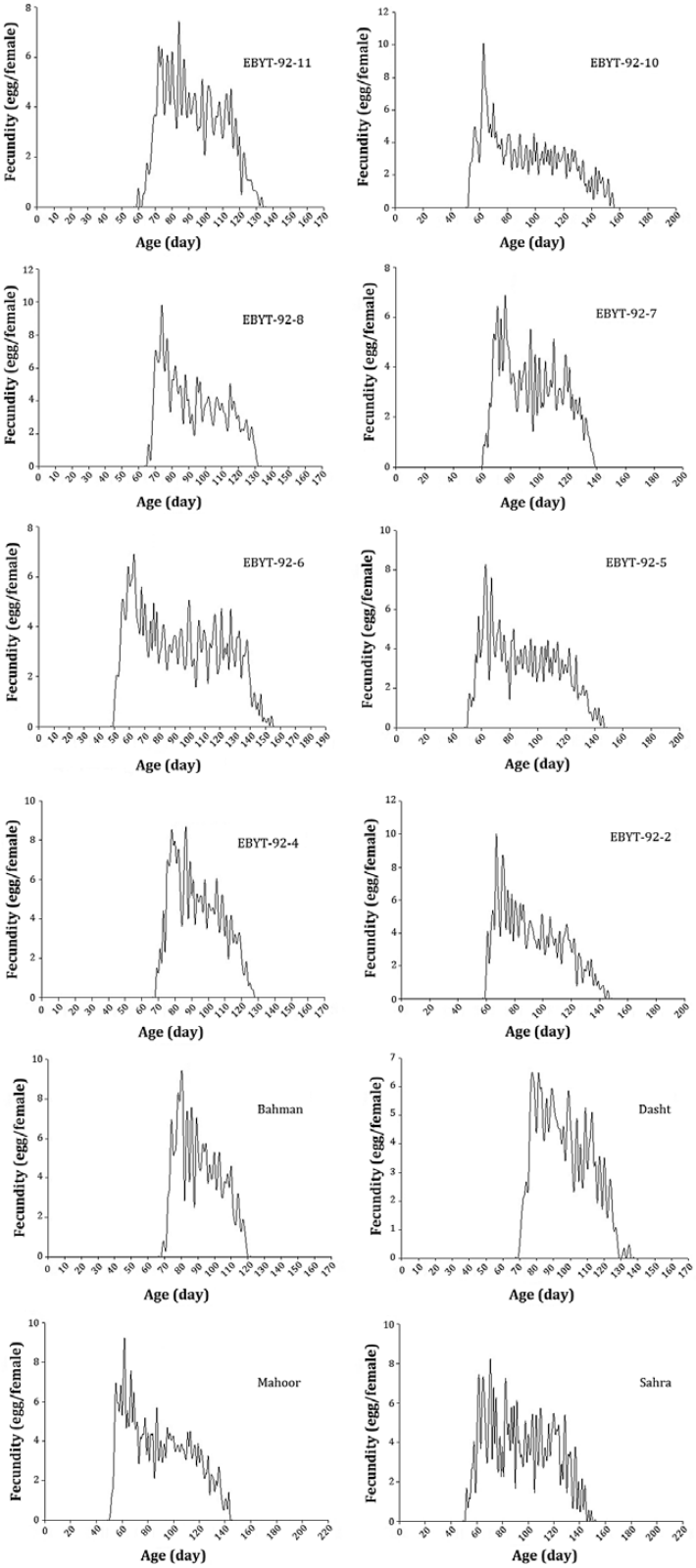

Fig. 2. Age-specific number of progeny per day (m_x) of *Rhyzopertha dominica* on various barley cultivars.

Digestive Enzymes Activity

Amylolytic ($F_{11,48}$ = 89.68; P < 0.001) and proteolytic ($F_{11,48}$ = 72.42; P < 0.001) activity measured for *R. dominica* reared on the 12 barley cultivars showed significant differences (Fig. 3). According to the results, the highest levels of α-amylase and general protease activity were recorded on cultivars Mahoor and EBYT-92-10, respectively. By contrast, the insects reared on cultivars Dasht had the lowest levels of α-amylase and general protease activity when compared with other barley cultivars tested.

Table 2. Mean (±SE) pre-oviposition and oviposition period and fecundity of *Rhyzopertha dominica* emerging from larvae fed on various barley cultivars

Barley cultivars	n^a	APOP (days)	TPOP (days)	Oviposition period (days)	Fecundity (eggs laid per female)
EBYT-92-2	20	12.35 ± 0.34b	64.15 ± 0.95c	42.15 ± 1.29cd	301.95 ± 7.66bc
EBYT-92–4	16	15.06 ± 0.39a	73.62 ± 0.89ab	32.93 ± 1.07ef	249.75 ± 9.37d
EBYT-92–5	21	7.23 ± 0.32d	56.19 ± 0.81f	48.52 ± 1.04bc	296.00 ± 5.77e
EBYT-92–6	23	7.13 ± 0.29d	54.30 ± 0.77fg	56.65 ± 1.09a	324.13 ± 6.99abc
EBYT-92–7	23	12.39 ± 0.40b	66.26 ± 0.77de	38.78 ± 0.76de	242.52 ± 3.86de
EBYT-92–8	20	13.00 ± 0.37b	68.60 ± 0.49cd	39.35 ± 1.02de	252.90 ± 6.70d
EBYT-92-10	20	8.10 ± 0.33cd	55.95 ± 0.87f	50.50 ± 1.43ab	316.45 ± 8.67abc
EBYT-92-11	19	13.05 ± 0.39ab	69.26 ± 1.01bcd	35.36 ± 1.21ef	234.63 ± 8.79ef
Bahman	15	12.13 ± 0.27b	73.06 ± 0.75abc	29.66 ± 0.94f	217.60 ± 7.11f
Dasht	15	13.86 ± 0.40ab	74.86 ± 1.12a	33.26 ± 0.95ef	221.93 ± 8.27f
Mahoor	26	7.37 ± 0.30d	53.84 ± 0.49g	55.15 ± 1.38a	338.61 ± 6.65ab
Sahra	20	9.65 ± 40c	57.70 ± 0.89f	41.45 ± 1.84de	348.05 ± 8.17a

The means followed by different letters in the same column are significantly different (Turkey's test, $P < 0.05$). APOP: Adult pre-oviposition period, TPOP: Total pre-oviposition period.

[a]The *n* value shows the sample size for each parameter.

Table 3. Mean (±SE) two-sex life table parameters of *Rhyzopertha dominica* fed on various barley cultivars

Barley cultivars	*GRR* (offspring)	R_0 (offspring)	r_m (day^{-1})	λ (day^{-1})	*T* (day)
EBYT-92-2	152.28 ± 2.10c	101.27 ± 1.82e	0.055 ± 0.002e	1.057 ± 0.001e	82.49 ± 0.53d
EBYT-92–4	123.12 ± 2.02f	67.97 ± 1.66i	0.047 ± 0.003i	1.048 ± 0.003i	89.19 ± 0.43b
EBYT-92–5	145.55 ± 2.05de	104.10 ± 1.84de	0.059 ± 0.004c	1.061 ± 0.001c	77.42 ± 0.40g
EBYT-92–6	166.14 ± 2.10b	123.99 ± 1.94b	0.062 ± 0.003b	1.065 ± 0.002b	76.33 ± 0.47h
EBYT-92–7	122.91 ± 1.79f	94.17 ± 1.65f	0.052 ± 0.001f	1.054 ± 0.004f	86.13 ± 0.35c
EBYT-92–8	141.87 ± 1.99e	85.00 ± 1.68g	0.051 ± 0.001g	1.052 ± 0.001g	86.55 ± 0.26c
EBYT-92-10	151.29 ± 2.09c	105.73 ± 1.81d	0.059 ± 0.002c	1.061 ± 0.002c	77.55 ± 0.48g
EBYT-92-11	127.70 ± 1.95f	74.88 ± 1.65h	0.049 ± 0.004h	1.050 ± 0.001h	86.72 ± 0.51c
Bahman	112.07 ± 1.87g	53.98 ± 1.52j	0.045 ± 0.002j	1.046 ± 0.003j	78.92 ± 0.32f
Dasht	107.04 ± 1.88g	55.12 ± 1.51j	0.043 ± 0.001k	1.044 ± 0.002k	91.72 ± 0.58a
Mahoor	176.40 ± 2.07a	146.79 ± 1.97a	0.066 ± 0.003a	1.066 ± 0.001a	80.62 ± 0.44i
Sahra	149.06 ± 2.13cd	116.34 ± 1.93c	0.058 ± 0.001d	1.060 ± 0.002d	74.41 ± 0.29c

The means followed by different letters in the same column are significantly different (Turkey's test, $P < 0.05$).

Physio-Chemical Characteristics of Barley Cultivars

The results of the starch and protein contents, seed hardiness, and one hundred-seed weight of various barley cultivars are shown in Table 4. No significant differences were observed in starch content ($F_{11,48} = 1.34$; $P = 0.231$) among the barley cultivars tested. The highest protein content ($F_{11,48} = 9.58$; $P < 0.001$) was measured in cultivars Sahra, Mahoor and EBYT-92-6, whereas the lowest content was in Dasht. The particle size index (PSI; as an indicator of grain hardness) significantly differed among the barley cultivars ($F_{11,48} = 12.64$; $P < 0.001$). The highest and lowest values of PSI were observed in cultivars Mahoor and Dasht, respectively. Also, the highest the mean hundred-seed weight was measured in cultivar EBYT-92-4, whereas the lowest content was detected in cultivar Bahman ($F_{11,48} = 19.94$; $P < 0.001$).

Correlation Analysis

The analysis of correlation coefficients of the fitness and digestive physiology of *R. dominica* reared on various barley cultivars with protein content, particle size index and hundred-seed weight of grains tested are shown in Table 5. The results of correlation coefficients showed that high negative correlation was found between immature stages and protein content and particle size index ($r = -0.835$ and -0.865, respectively). Moreover, a positive correlation was found between male and female longevity and protein content ($r = 0.751$ and 0.791, respectively) and particle size index ($r = 0.801$ and 0.833, respectively). Very high positive correlations were given between *GRR* ($r = 0.890$), R_0 ($r = 0.940$), r_m ($r = 0.933$), and λ ($r = 0.915$), with particle size index. The correlation coefficients showed that amylolytic ($r = 0.922$) and proteolytic ($r = 0.839$) activities exhibited positive correlation with particle size index. There was no significant correlation between the fitness and digestive physiology of *R. dominica* with protein content and particle size index of various barley cultivars.

Discussion

Several studies have indicated that the various cultivars of grains influence development, longevity and reproductive variables of stored-product pests (Chougourou et al. 2013, Borzoui and Naseri 2016, Naseri and Borzoui 2016, Golizadeh and Abedi 2017). The results of present study suggest that *R. dominica* fed on the 12 barley cultivars tested is able to complete its development period and reproduction at the different rates. Furthermore, the present study demonstrates the existence of interactions between physio-chemical characteristics of seeds on the growth and life table parameters of this pest.

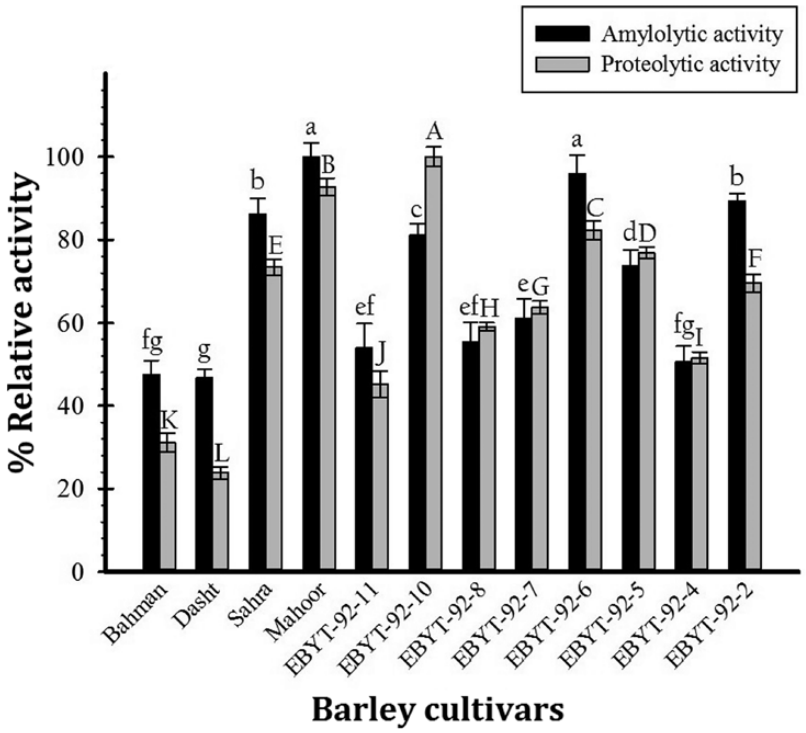

Fig. 3. Mean (±SE) relative amylolytic and proteolytic activity of gut extracts from *Rhyzopertha dominica* reared on various barley cultivars. The error bars indicate standard error of the mean of five replicate experiments. Letters above the bars indicate statistically significant differences between values (Turkey's test, $P < 0.05$).

Table 4. Mean (±SE) physico-chemical characteristics ($n = 5$) of barley cultivars tested

Barley cultivars	Starch content (mg/g)	Protein content (mg/g)	Particle size index (%)	Hundred-seed weight (mg)
EBYT-92-2	295.73 ± 9.96a	58.06 ± 1.72bcd	18.23 ± 1.06bc	4.60 ± 0.16ab
EBYT-92–4	300.12 ± 8.78a	52.76 ± 1.92cd	16.43 ± 1.05bc	4.81 ± 0.11a
EBYT-92–5	303.23 ± 10.53a	61.74 ± 3.27bc	18.81 ± 0.92b	4.70 ± 0.06a
EBYT-92–6	319.88 ± 6.42a	77.05 ± 4.89a	20.97 ± 0.87ab	4.62 ± 0.11ab
EBYT-92–7	305.30 ± 11.56a	53.59 ± 3.03cd	19.33 ± 0.99b	4.72 ± 0.10a
EBYT-92–8	299.73 ± 10.37a	57.31 ± 3.45cd	16.81 ± 1.22bc	4.78 ± 0.09a
EBYT-92-10	318.77 ± 13.53a	67.15 ± 3.63b	20.71 ± 1.04ab	4.71 ± 0.16a
EBYT-92-11	309.98 ± 7.65a	54.68 ± 4.00cd	16.81 ± 0.77bc	4.56 ± 0.14ab
Bahman	286.72 ± 14.35a	57.00 ± 3.32cd	13.33 ± 1.00cd	3.84 ± 0.27d
Dasht	303.09 ± 7.42a	51.56 ± 3.04d	11.14 ± 0.65d	4.37 ± 0.12bc
Mahoor	331.61 ± 14.92a	78.62 ± 3.80a	24.96 ± 1.22a	4.17 ± 0.17c
Sahra	294.43 ± 10.40a	78.79 ± 3.00a	18.85 ± 1.12b	4.22 ± 0.12c

The means followed by different letters in the same column are significantly different (Turkey's test, $P < 0.05$).

Table 5. Correlation coefficients (r) of life table parameters and physiological characteristics of *Rhyzopertha dominica* fed on various barley cultivars with protein content, particle size index and hundred-seed weight

Parameter	Protein content		Particle size index		Hundred-seed weight	
	r	P_{value}	r	P_{value}	r	P_{value}
Immature stages	–0.835	0.001	–0.865	0.000	–0.125	0.699
Male longevity	0.751	0.005	0.801	0.002	0.293	0.355
Female longevity	0.791	0.002	0.833	0.001	0.019	0.953
Fecundity	0.900	0.000	0.799	0.002	0.008	0.980
GRR	0.830	0.001	0.890	0.000	0.099	0.758
R_0	0.857	0.000	0.940	0.000	0.053	0.870
r_m	0.855	0.000	0.933	0.000	0.072	0.824
λ	0.848	0.000	0.915	0.000	0.110	0.733
T	–0.784	0.000	–0.531	0.076	0.297	0.348
Amylolytic activity	0.725	0.008	0.922	0.000	0.279	0.379
Proteolytic activity	0.853	0.000	0.839	0.001	–0.020	0.952

In this study, the incubation period of *R. dominica* showed a significant difference among the 12 barley cultivars that is somewhat in agreement with the finding of Howe (1950) and Thompson (1966), who reported that the incubation period of *R. dominica* varied from 7 to 11 d on various grains.

The results of this study indicate that the development of *R. dominica* immature stages differed significantly on the 12 cultivars of barley studied. This coleopteran pest developed slower on Bahman, Dasht, and EBYT-92-4, suggesting that the nutritional quality of these cultivars is less suitable for *R. dominica* feeding. There is a negative correlation between the duration of immature stages of this pest and the seed hardness (r = –0.865) of barley cultivars tested. Astuti et al. (2013) and Suits et al. (2017) reported that the quality of feed for animals is considered to be critical factors that affect feeding preference and performance of insect pests.

The interactions of macronutrients with other dietary characteristics to influence lifespan and reproduction are complex (Coskun et al. 2005, Chen et al. 2009). It has been proposed that low nutritive quality of host diet is one possible measure offering resistance against insect herbivores (Lee et al. 2004, Borzoui et al. 2015). This is illustrated by the present study, in which it was found that the adult longevity and fecundity of *R. dominica* fed on barley cultivars were positively correlated to the protein content and seed hardness (Table 5), suggesting that these factors play a decisive role in the fitness of this insect. Similar effects of seed hardness have been reported for *Sitotroga cerealella* (Olivier; Lepidoptera: Gelechiidae) (Borzoui et al. 2017) and *R. dominica* (Toews et al. 2001).

Our results reveal that, in addition to its impacts on developmental time, the various barley cultivars also influences the age-stage specific survival rate of the lesser grain borer, demonstrating that the highest and lowest survival rate of immature stages were recorded on cultivars Mahoor and Dasht, respectively. Similar results were observed by Chougourou et al. (2013), with *R. dominica* reared on some rice varieties.

A population projection based on an age-stage, two-sex life table can show the stage structure change during growth of population. Understanding stage structure is necessary to the management of insect pests because their dispersal and damage capability varies with stage. The present study reveals that such a life table can provide a comprehensive description of the performance of *R. dominica* population on the various barley cultivars. The reduced R_0, *GRR*, and λ of this pest found on cultivar Dasht might be attributed to the positive correlation of these factors with the protein content and seed hardness of tested cultivars (Table 5). Astuti et al. (2013) showed that the physico-chemical characteristics of milled rice varieties are the effective factor on the development of *R. dominica*.

The intrinsic rate of natural increase (r_m) is an important parameter, describing the growth potential of a population under food conditions because it summarizes all differences in developmental time, survival rate, and reproduction of the population (Southwood 1978, Carey 1993). Normally, higher r_m is related to shorter developmental time, lower mortality, and greater fecundity (Razmjou et al. 2014, Borzoui et al. 2016), which is true for *R. dominica* reared on Mahoor. Probably, the variation in r_m values of insects reared on the different barley cultivars resulted from chemical and physical differences between the cultivars. A higher population of *R. dominica* on cultivar Mahoor can increase their damage (number of damaged grains and weight losses) on this cultivar, as reported by Chougourou et al. (2013). They found that NRICA8 and NERICA10 had the highest percentage of weight losses as they did with *R. dominica* population during 2 and 3 mo of storage.

A common result is that the host diet appears to be an important factor in the synthesis and secretion of the digestive enzymes (Bouayad et al. 2008, Lomate and Hivrale 2011). Our studies showed highest gut amylolytic activity in Mahoor-fed insects, i.e., the gut amylolytic levels was proportional to the protein content (r = 0.725) and hardness (r = 0.922) of seeds. *R. dominica* digestive gut proteases are complex, diverse, and flexible when exposed to various barley cultivars. When fed on the softer cultivars (Mahoor, EBYT-92-10 and EBYT-92-6), the gut proteinase levels was up-regulated. On the contrary, *R. dominica* fed on the harder cultivars (Dasht and Bahman) showed down-regulation of the digestive proteinase. These results are comparable to earlier findings of Borzoui et al. (2017), which reported high *S. cerealella* amylolytic activity on grains with low seed hardness. Several other insects also show a dynamic evolutionary variation in gene clusters of digestive α-amylases and proteases, pointing towards their importance in the digestive physiology (Chougule et al. 2001, Bin et al. 2011, Piasecka-Kwiatkowska et al. 2014).

In conclusion, delayed development and reduced survival rate exhibited by insects fed on cultivars Dasht and Bahman indicate that these cultivars were of poorer quality, demographically than the other barley cultivars. Correlation coefficients analysis showed that digestive enzymes activity correlates to the protein content and seed hardness. We concluded that the physio-chemical characteristics of seeds together with the level of gut digestive enzymes resulted in considerable effects on the fitness of *R. dominica*. This study helps us in understanding the extent of digestive and flexibility in development that *R. dominica* possesses.

Any further pest control strategy developed using the transgenic crop or gene silencing approach can turn out to be sustainable when this adaptive dynamism is taken into consideration. The use of genes that encode insecticidal characteristics in transgenic plants has the potential to benefit the production agricultural crop, the consumer, and the environment and will come from the reduced use of chemical sprays. Also, these characteristics allow only the pests of the crop to be targeted.

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References Cited

AACC. 2000. Approved methods of the American Association of Cereal Chemists, 10th ed. The American Association of Cereal Chemists, St Paul, MN.

Astuti, L. P., G. Mudjiono, C. S. Rasminah, and B. T.Rahardjo. 2013. Susceptibility of milled rice varieties to the lesser grain borer (*Rhyzopertha dominica*, F). J. Agric. Sci. 5: 145–149.

Bernfeld, P. 1955. Amylases, α and β. Methods Enzym. 1: 149–158.

Bin, Z., L. Huai, H. Hull-Sanders, and W.Jin-jun. 2011. Effect of host plants on development, fecundity and enzyme activity of *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae). Agri. Scie. China. 10: 1232–1240

Boeke, S. J. 2002. Traditional African plant products to protect stored cowpeas against insect damage; the battle against the beetle. PhD Thesis. Wageningen University, p. 151.

Borzoui, E., and A. R. Bandani. 2013. Wheat and triticale proteinaceous seed extracts inhibit gut α-amylase and protease of the carob moth, *Ectomyelois ceratoniae*. Mol. Entomol. 4: 13–21.

Borzoui, E., and B. Naseri. 2016. Wheat cultivars affecting life history and digestive amylolytic activity of *Sitotroga cerealella Olivier* (Lepidoptera: Gelechiidae). Bull. Entomol. Res. 106: 464–473.

Borzoui, E., B. Naseri, and F. R. Namin. 2015. Different diets affecting biology and digestive physiology of the Khapra beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae). J. Stored Prod. Res. 62: 1–7.

Borzoui, E., B. Naseri, Z. Abedi, and M. S. Karimi-Pormehr. 2016. Lethal and sublethal effects of essential oils from *artemisia khorassanica* and *vitex*

pseudo-negundo against *plodia interpunctella* (Lepidoptera: Pyralidae). Environ. Entomol. 45: 1220–1226.

Borzoui, E., B. Naseri, and G. Nouri-Ganbalani. 2017. Effects of food quality on biology and physiological traits of *sitotroga cerealella* (Lepidoptera: Gelechiidae). J. Econ. Entomol. 110: 266–273.

Bouayad, N., K. Rharrabe, N. Ghailani, and F.Sayah. 2008. Effects of different food commodities on larval development and α-amylase activity of *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae). J. Stored Prod. Res. 44: 373–378.

Bradford, M. M. 1976. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Anal. Biochem. 72: 248–254.

Carey, J. R. 1993. Applied demography for biologists with special emphasis on insects. Oxford University Press, New York, NY.

Chen, Y., X. Ni, and G. D. Buntin. 2009. Physiological, nutritional, and biochemical bases of corn resistance to foliage-feeding fall armyworm. J. Chem. Ecol. 35: 297–306.

Chi, H., and H. Y. Su. 2006. Age-stage, two-sex life tables of *Aphidius gifuensis* (Ashmead) (Hymenoptera: Braconidae) and its host *Myzus persicae* (Sulzer) (Homoptera: Aphididae) with mathematical proof of the relationship between female fecundity and the net reproductive rate. Environ. Entomol. 35: 10–21.

Chougourou, D. C., A. Togola, F. E. Nwilene, J. Adeliossi, F. Bachabi, and O. E.Oyetunji. 2013. Susceptibility of some rice varieties to the lesser grain borer, *Rhyzopertha dominica* Fab. (Coleoptera: Bostrichidae) in Benin. J. Appl. Sci. 13: 173–177.

Collins, P. J. 2006. Resistance to chemical treatments in insect pests of stored grain and its management. *In* I. Lorini, B. Bacaltchuk, H. Beckel, D. Deckers, E. Sundfeld, J. P. dos Santos, J. D. Biagi, J. C. Celaro, L. R. D'A Faroni, O. F. Bortolini Lde, M. R. Sartori, M. C. Elias, R. N. C. Guedes, R. G. da Fonseca, and V. M. Scussel. (eds.), Proceedings of the 9th International Working Conference on Stored Product Protection, 15–18 October 2006, Sao Paulo, Brazil, pp. 277–282.

Coskun, M., P. Ozalp, M. Sulanc, and I.Emre. 2005. Effects of various diets on the oviposition and sex ratio of *Pimpla turionellae* L. Int. J. Agri. Biol. 7: 129–132.

Cuperus, G., V.Krischik. 1995. Why stored product integrated pest management is needed. *In* W. Krischik, G. Cuperus, and D. Galliart (eds.), Stored product management, Vol. E-912. Oklahoma State University Cooperative Extension Service Circular. Oklahoma Cooperative Extension Service, Stillwater, OK. p. 199.

Deans, C. A., G. A. Sword, and S. T. Behmer. 2015. Revisiting macronutrient regulation in the polyphagous herbivore *Helicoverpa zea* (Lepidoptera: Noctuidae): New insights via nutritional geometry. J. Insect Physiol. 81: 21–27.

Edde, P. A. 2012. A review of the biology and control of *Rhyzopertha dominica* (F.) the lesser grain borer. J. Stored Prod. Res. 48: 1–18.

Efron, B., and R. J.Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, NY, 436 pp.

Elpidina, E. N., K. S. Vinokurov, V. A. Gromenko, Y. A. Rudenskaya, Y. E. Dunaevsky, and D. P. Zhuzhikov. 2001. Compartmentalization of proteinases and amylases in *Nauphoeta cinerea midgut*. Arch. Insect Biochem. Physiol. 48: 206–216.

Fargo, W. S., D. Epperly, G. W. Cuperus, B. C. Clary, and R.Noyes. 1989. Effect of temperature and duration of trapping on four stored grain insect species. J. Econ. Entomol. 82: 970–973.

Fouad, H. A., L. R. D'Antonino Faroni, E. R. de Lima, and E. F.Vilela. 2013. Relationship between physical-chemical characteristics of corn seeds and susceptibility to *Sitotroga cerealella*. Maydica. 58: 169–172.

Golizadeh, A., and Z. Abedi. 2017. Feeding performance and life table parameters of Khapra Beetle, *Trogoderma granarium* Everts (Coleoptera: Dermestidae) on various barley cultivars. Bull. Entomol. Res. 107: 689–698.

Hagstrum, D. W., and B.Subramanyam. 1996. Integrated management of insects in stored products. Marcel Dekker, Inc, New York, NY.

Hosseininejad, S., and B. Naseri. 2015. Nutritional and growth indices of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on different corn hybrids. Arthropod. Plant Interact. 9: 633–640.

Howe, R. W. 1950. The development of *Rhyzopertha dominica* (F.) (Coleoptera: Bostrichidae) under constant temperature. Entomol. Mag. 86: 1–5.

Huang, Y. B., and H.Chi. 2013. Life tables of *Bactrocera cucurbitae* (Diptera: Tephritidae): with an invalidation of the jackknife technique. J. Appl. Entomol. 137: 327–339.

La Rossa, F. R., A. Vasicek, and M. C. López. 2013. Effects of pepper (*Capsicum annuum*) cultivars on the biology and life table parameters of *myzus persicae* (Sulz.) (Hemiptera: Aphididae). Neotrop. Entomol. 42: 634–641.

Lee, K. P., D.Raubenheimer, and S. J. Simpson. 2004. The effects of nutritional imbalance on compensatory feeding for cellulose-mediated dietary dilution in a generalist caterpillar. Physiol. Entomol. 29: 108–117.

Lomate, P. R., and V. K. Hivrale. 2011. Differential responses of midgut soluble aminopeptidases of *Helicoverpa armigera* to feeding on various host and non-host plant diets. Arthropod. Plant Interact. 5: 359–368.

Majd-Marani, S., B. Naseri, G. Nouri-Ganbalani, and E. Borzoui. 2017. The effect of maize hybrid on biology and life table parameters of the *Trogoderma granarium* (Coleoptera: Dermestidae). J. Econ. Entomol. 110: 1916–1922.

McKevith, B. 2004. Nutritional aspects of cereals. Nutr. Bull. 29: 111–142.

Naseri B., and E.Borzoui. 2016. Life cycle and digestive physiology of *Trogoderma granarium* (Coleoptera: Dermestidae) on various wheat cultivars. Ann. Entomol. Soc. Am. 109: 831–838.

Patankar, A. G., A. P. Giri, A. M. Harsulkar, M. N. Sainani, V. V. Deshpande, P. K. Ranjekar, and V. S. Gupta. 2001. Complexity in specificities and expression of *Helicoverpa armigera* gut proteinases explains polyphagous nature of the insect pest. Insect Biochem. Mol. Biol. 31: 453–464.

Piasecka-Kwiatkowska, D., and J. R. Warchalewski. 2000a. The cereal protein inhibitors of hydrolytic enzymes and their role. Part I. Protein inhibitors of α-amylase. Zywnos´c´. 2: 110–119 (in Polish).

Piasecka-Kwiatkowska, D., and J. R.Warchalewski. 2000b. The cereal protein inhibitors of hydrolytic enzymes and their role. Part II. Protein inhibitors of proteinases. Zywnos´c´. 3: 33–38 (in Polish).

Piasecka-Kwiatkowska, D., J. Nawrot, M. Zielinska-Dawidziak, M. Gawlak, and M.Michalak. 2014. Detection of grain infestation caused by the granary weevil (*Sitophilus granarius* L.) using zymography for α-amylase activity. J. Stored Prod. Res. 56: 43–48.

Raubenheimer, D., and S. J.Simpson. 2004. Organismal stoichiometry: quantifying non-independence among food components. Ecology. 85: 1203–1216.

Razmjou, J., B. Naseri, and S. A.Hemati. 2014. Comparative performance of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae) on various host plants. J. Pest Sci. 87: 29–37.

SAS. 2011. SAS® software version 9.3, user's manual. SAS Institute, Cary, NC.

Southwood, T. R. E. 1978. Ecological methods. Chapman and Hall, New York, NY.

Suits, R., D. Reisig, and H. Burrack. 2017. Feeding preference and performance of *Helicoverpa zea* (Lepidoptera: N octuidae) larvae on various soybean tissue types. Fla. Entomol. 100: 162–167.

Thompson, V. 1966. Biology of the lesser grain borer, *Rhyzopertha dominica* (F). Bull. Grain Technol. 4: 163–168.

Toews, M. D., G. W. Cuperus, and T. W. Phillips. 2000. Susceptibility of eight U.S. wheat cultivars to infestation by *Rhyzopertha dominica* (Coleoptera: Bostrichidae). Environ. Entomol. 29: 250–255.

Toews, M. D., T. W. Phillips, and G. W. Cuperus. 2001. Effects of wheat cultivar and temperature on suppression of *Rhyzopertha dominica* (Coleoptera: Bostrichidae) by the parasitoid *Theocolax elegans* (Hymenoptera: Pteromalidae). Biol. Control. 21: 120–127.

Vela-Coiffier, E. L., W. S. Fargo, E. L. Bonjour, G. W. Cuperus, and W. D.Warde. 1997. Immigration of insects into on-farm stored wheat and relationships among trapping methods. J. Stored Prod. Res. 33: 157–166.

Watts, V. M., and F. V. Dunkel. 2003. Postharvest resistance in hard spring and winter wheat varieties of the northern great plains to the lesser grain borer (Coleoptera: Bostrichidae). J. Econ. Entomol. 96: 220–230.