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The life table parameters of *Megalurothrips usitatus* (Thysanoptera: Thripidae) on four leguminous crops

Liang-De Tang¹, Kai-Li Yan¹, Bu-Li Fu¹, Jian-Hui Wu², Kui Liu^{1,*}, and Yong-Yue Lu^{1,2,*}

Abstract

The bean flower thrips, *Megalurothrips usitatus* (Thysanoptera: Thripidae), is an important pest of leguminous crops (Fabales: Fabaceae) in south China. In this study, life history parameters of *M. usitatus* were investigated on 4 leguminous crops: snap bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* (L.) Walp.), pea (*Pisum sativum* L.), and lima bean (*Phaseolus limensis* Macf.). The development times (mean \pm SE) from egg to adult on snap bean, cowpea, pea, and lima bean pods were 9.53 ± 0.06 , 10.62 ± 0.14 , 11.20 ± 0.11 and 11.55 ± 1.13 days, respectively. Survivorship of immatures was high on snap bean (80%) but low on lima bean (48%). The total number of first instars produced was highest on snap bean (sexual reproduction: 112.15 ± 11.98 ; parthenogenesis: 195.89 ± 19.24), and lowest on lima bean (sexual reproduction: 42.17 ± 2.99 ; parthenogenesis: 49.50 ± 3.90). *Megalurothrips usitatus* had the highest intrinsic rate of increase (r_m) on snap bean (0.205), followed by cowpea (0.181), pea (0.171), and lima bean (0.125). The results indicate that snap bean was the most suitable host plant for *M. usitatus*, whereas lima bean was the least suitable.

Key Words: *Megalurothrips usitatus*; life history; leguminous crops; development; survival rate

Resumen

Los trips de las flores de frijol, *Megalurothrips usitatus* (Thysanoptera: Thripidae), son una plaga importante de cultivos leguminosos (Fabales: Fabaceae) en el sur de China. En este estudio, los parámetros de historia de vida de *M. usitatus* fueron investigados en 4 legumbres: habichuela (*Phaseolus vulgaris* L.), caupí (*Vigna unguiculata* (L.) Walp.), arveja (*Pisum sativum* L.) y frijol lima (*Phaseolus limensis* Macf.). El tiempo de desarrollo de huevo a adulto en las vainas de habichuela, caupí, arveja y frijol lima fue 9.53 ± 0.06 , 10.62 ± 0.14 , 11.20 ± 0.11 y 11.55 ± 1.13 días, respectivamente. La sobrevivencia de inmaduros en habichuela fue alta (80%) pero baja en el frijol lima (48%). El número total de larvas del primer estadio producido fue más alto en la habichuela (reproducción bisexual: 112.15 ± 11.98 ; partenogénesis: 195.89 ± 19.24), mientras que fue el más bajo en frijol lima (reproducción bisexual: 42.17 ± 2.99 ; partenogénesis: 49.50 ± 3.90). *Megalurothrips usitatus* tuvo la tasa intrínseca de crecimiento (r_m) más alta en habichuela (0.205), seguido por caupí (0.181), arveja (0.171) y el frijol lima (0.125). Los resultados indican que la habichuela fue la planta hospedera más adecuada para *M. usitatus*, mientras que el frijol lima fue el menos adecuado.

Palabras Clave: *Megalurothrips usitatus*; historia de vida; legumbres; desarrollo; tasa de sobrevivencia

The bean flower thrips, *Megalurothrips usitatus* (Bagnall) (Thysanoptera: Thripidae), which recently infested southern China, poses an economic threat to a wide range of leguminous plants (Fabales: Fabaceae), especially to snap bean, *Phaseolus vulgaris* L., and cowpea, *Vigna unguiculata* (L.) Walp. Thrips damage is caused by direct feeding on the contents of individual plant cells and the consequent reduction of photosynthetic capacity (Shipp et al. 2000). Losses caused by petal and fruit malformation and scarring are of even greater economic importance (Zhang et al. 2007). The flowering stage of the crops is particularly vulnerable to this pest. Thrips occur every growing season and cause yield losses through premature dropping of flowers. Also, pod necrosis caused by feeding and oviposition can significantly reduce the market value of crops. The yield loss in peanut caused by the feeding damage of *M. usitatus* and other thrips, i.e., *Scirtothrips dorsalis* Hood and *Thrips* spp., has been estimated to be about 30% (Chen 1980). Although the relationships between *M. usitatus* infestation and yield losses of various leguminous crops are not clearly known, serious damage by *M. usitatus* on leaves, flowers and pods of various leguminous

crops done has been noted. Dozens to hundreds of adults and nymphs per flower may be found at peak pest occurrence on cowpea (Fan et al. 2013) and on snap bean.

It is important to learn the biological attributes of a new insect pest in order to understand its potential spread (Morse & Hoddle 2006). To date, little is known about the biology and ecology of *M. usitatus*, of which there was a recent outbreak in southern China. However, several biological studies of this pest thrips have been conducted in Taiwan, China (Chang 1987, 1988a, 1988b, 1992). Suitability assessments made by offering various host plants helped us gain understanding of the feeding and/or oviposition behaviors (Dethier et al. 1960), the resistance of host plants (Painter 1951), other relationships of insects and plants (Chang 1988), as well as to serve as a guide to pest control (van Rijn et al. 1995).

In south China, a tropical and subtropical area, many leguminous crops can be grown at the same time throughout the year. In order to ascertain the relationships of *M. usitatus* with various leguminous crops, and to acquire a better understanding of its potential threat to

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important leguminous crops, we studied the suitability to *M. usitatus* of 4 leguminous vegetable plant species: snap bean (*Phaseolus vulgaris* L.), cowpea (*Vigna unguiculata* (L.) Walp.), pea (*Pisum sativum* L.), and lima bean (*Phaseolus limensis* Macf.). The objective was to investigate whether *M. usitatus* could complete its development on pods, and to compare its developmental parameters and population growth potentials on these 4 important crops.

Materials and Methods

INSECT REARING AND PREPARATION

The population of the bean flower thrips originated in 2013 from a cowpea field at Haikou, China. This population was subsequently reared by the bean pod method (Mollema et al. 1993). The colony was kept at 26 ± 1 °C, 75% RH and 16: 8 h L:D in a climate control chamber.

DEVELOPMENT AND IMMATURE SURVIVAL

Initially, 6 fresh pods of the same leguminous species were transferred into a single glass jar used for rearing, each containing hundreds of adult thrips. Adult females were allowed to oviposit on the pods for 12 h. Thereafter, the adults were removed and each egg-bearing pod was placed in a Petri dish (9 cm diam) with the bottom covered by a water-soaked filter paper to prevent desiccation of the eggs and the pod. The Petri dishes were then held in a climate control chamber at 26 ± 1 °C, 75% RH, and 16:8 h L:D until larvae hatched from the eggs. Because thrips eggs are laid into the pod tissue, the egg development period was determined by recording the passage of time until the appearance of larvae, but egg mortality could not be determined (van Rijn et al. 1995; Zhang et al. 2007; Park et al. 2010). In each treatment, 100 newly hatched larvae were transferred using a fine hair bush into each 4 mL centrifuge tube containing a 2 cm length of pod. Each centrifuge tube was sealed with a cotton plug to prevent thrips from escaping. Each such tube constituted a replicate. Pods of each species of test legume were replaced with fresh ones every 3 days. Immature stage development and survival were assessed at 12 h intervals until the larvae either died or matured. Dead individuals of any developmental stage were not included when calculating the average developmental time at a specific stage. The various immature instars were identified by the method elaborated by Zhang et al. (2007).

DURATIONS OF PREOVIPOSITION, OVIPOSITION, AND POSTOVIPOSITION PERIODS, SEX RATIOS, AND ADULT LONGEVITIES

For the sexual reproduction experiment, about 30 pairs of newly emerged adults in each treatment were collected and each pair was

placed in a glass tube (2.5 cm diam, 8.0 cm length) containing a fresh pod as described above. The pods were changed daily and the replacement pods were individually transferred into a new single glass tube and the lids were sealed with a cotton plug. The number of live adults of each sex was recorded until all adults had died. The number of the first instars that hatched on each individual replacement pod was counted and used to calculate the daily fecundity of females (Watts 1934). The offspring were reared to adulthood using the methods described above. The numbers of females and males were recorded to estimate the sex ratios of the offspring. The pre-oviposition period, oviposition period, post-oviposition period, the number of first instars per female per day, the number of first instars laid per female during her lifetime, and adult longevity were also recorded.

In the parthenogenetic reproduction experiment, about 30 newly emerged female adults in each treatment were used, and each female was placed in a glass tube with a segment of bean pod. Each tube constituted a replication. The parameters of the same biologic attributes as in the sexual reproduction experiment were recorded as described above.

LIFE TABLE PARAMETERS

Net reproductive rate (R_0), intrinsic rate of increase (r_m), finite rate of increase (λ), generation time (T) and doubling time (DT) were calculated from the data of survival rates and fecundity described above, and were calculated according to the methods of Birch (1948).

STATISTICAL ANALYSIS

A one-way analysis of variance (ANOVA) was used to analyze for significant differences ($P < 0.05$) in development time, survivorship of the immatures, longevity, and reproduction of the adults among leguminous crops. Data were analyzed using SPSS software (SPSS 10.0, 2000), and the differences were compared using the Tukey multiple range test when the diet effect was significant ($P < 0.05$) (SPSS 10.0, 2000). A chi-square test was used to examine the departure of sex ratio from 1:1 (SPSS 10.0, 2000).

Results

IMMATURE DEVELOPMENT AND SURVIVORSHIP

There were significant differences in the life spans of the various developmental stages fed on various leguminous crop pods (first instar: $F=25.361$, $df=3$, 378, $P=0.018$; second instar: $F = 2.676$, $df = 3$, 324, $P = 0.002$; prepupa: $F = 3.315$, $df = 3$, 288, $P < 0.001$; pupa: $F = 18.269$, $df = 3$, 249, $P < 0.001$; Table 1). The egg-hatching time was

Table 1. The development time^a (days; mean \pm SE) of *Megalurothrips usitatus* on snap bean, cowpea, pea, and lima bean. Numbers in parentheses are live insects at that developmental stage.

Crop	Development time in days \pm SE					
	Egg	First instar larva	Second instar larva	Prepupa	Pupa	Egg to adult
Snap bean	2.89 \pm 0.04 c (100)	1.69 \pm 0.03 b (99)	2.89 \pm 0.03 b (97)	0.95 \pm 0.03 b (92)	1.69 \pm 0.04 b (80)	9.53 \pm 0.06 d (80)
Cowpea	3.02 \pm 0.04 b (100)	1.68 \pm 0.03 b (98)	2.90 \pm 0.05 b (83)	1.05 \pm 0.02 a (76)	2.13 \pm 0.06 a (66)	10.62 \pm 0.14 c (66)
Pea	3.29 \pm 0.03 a (100)	1.73 \pm 0.03 b (94)	2.97 \pm 0.05 ab (75)	1.06 \pm 0.04 a (68)	2.19 \pm 0.09 a (59)	11.20 \pm 0.11 b (59)
Lima bean	3.35 \pm 0.04 a (100)	2.02 \pm 0.04 a (91)	3.05 \pm 0.05 a (73)	1.06 \pm 0.04 a (56)	2.27 \pm 0.09 a (48)	11.55 \pm 1.13 a (48)

^aMean values within the same column followed by different letters are significantly different by Tukey's multiple range test ($P < 0.05$).

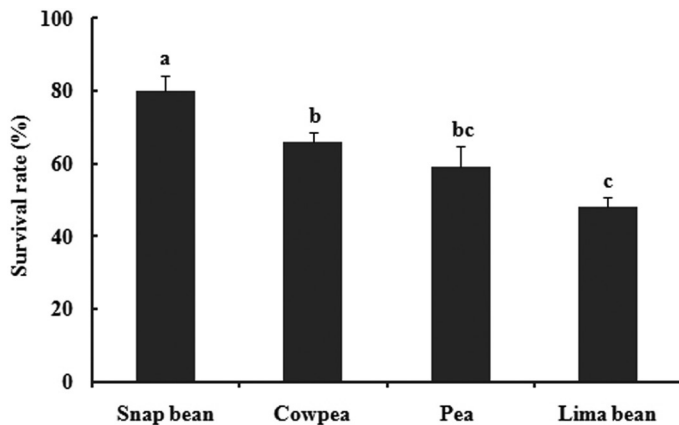


Fig. 1. Mean (\pm SE) survival rate of *Megalurothrips usitatus* on 4 leguminous crops. Means values with same letter are not significantly different by Tukey's multiple range test ($P < 0.05$).

shorter on snap bean compared to cowpea, pea, and lima bean. The development times of the 2 larval stages (first and second instar larvae) were longer on lima bean than on snap bean, cowpea, and pea, but were not significantly different among snap bean, cowpea, and pea. The prepupa and pupa developed more rapidly on snap bean than on the other 3 leguminous vegetables. However, no significant differences in development time were found among cowpea, pea, and lima bean. Taken together, the development time from egg to adult was shortest on snap bean, and was only 82.5% of that on lima bean.

Leguminous host crop pods had a significant impact on the survivorship of the immature stages ($F = 18.419$, $df = 3$, $P < 0.001$) (Fig. 1). The survivorship of *M. usitatus* was significantly less on lima bean (48%) and greater on snap bean (80%). For all leguminous host plant pods, the mean survival rates decreased in the following order: snap bean > cowpea > pea > lima bean (Fig. 1).

ADULT LONGEVITY

The longevity of adult females and males varied significantly when they were reared as larvae on these different crops (sexual reproduction: female: $F = 1.591$, $df = 3$, 102 , $P = 0.002$; male: $F = 38.306$, $df = 3$, 107 , $P = 0.022$; parthenogenesis: $F = 8.359$, $df = 3$, 103 , $P < 0.001$) (Table 2). The longevity of adult females reproducing by parthenogenesis was significantly longer on snap bean than on the other tested

leguminous crops, and averaged longer for those reproducing sexually. Similar results were found in the longevities of adult males, but they had a shorter longevity than females. The oviposition period showed the same trend, longest on snap bean (sexual reproduction: 13.19 ± 0.80 d; parthenogenesis: 18.11 ± 1.19 d), and shortest on lima bean (sexual reproduction: 10.63 ± 0.49 d; parthenogenesis: 11.87 ± 0.56 d). On lima bean, females had relatively longer pre-oviposition and post-oviposition periods (though not always significantly so) than on the other 3 leguminous species tested, and represented < 30% of adult female longevity.

FECUNDITY AND SEX RATIO

Overall, the pattern of age-dependent fecundity was similar on all the 4 leguminous crops tested (Fig. 2). The estimated number of eggs laid per day peaked shortly after the beginning of the oviposition period, followed by a steady decline. However, there were significant differences in fecundity (sexual reproduction: $F = 21.438$, $df = 3$, 102 , $P < 0.001$; parthenogenesis: $F = 37.709$, $df = 3$, 104 , $P < 0.001$) among the 4 leguminous plants tested (Table 3). Fecundity was represented by the number of first instar larvae produced by each female. The greatest fecundity was observed on snap bean (sexual reproduction: 112.15 ± 11.98 eggs/female; parthenogenesis: 195.89 ± 19.24 eggs/female), and it was the smallest on lima bean (sexual reproduction: 42.17 ± 2.99 eggs/female; parthenogenesis: 49.50 ± 3.90 eggs/female). The offspring per female when thrips were reared on snap bean was nearly 3-fold and 4-fold higher than on lima bean in sexual reproduction and parthenogenesis, respectively. The mean fecundity of thrips decreased on the leguminous host plants in following order: snap bean > cowpea > pea > lima bean. There was no significant difference in the sex ratio, with the proportion of females ranging from 0.44-0.49 ($\chi^2 = 3.057$, $P = 0.383 > 0.05$).

POPULATION GROWTH PARAMETERS

The population growth parameters of *M. usitatus* reared on the tested leguminous host plants are given in Table 4. The net reproductive rate (R_0) was calculated as the predicted number of the first instar larvae in the next generation. The greatest R_0 -value was found on snap bean (40.333), whereas the smallest was on lima bean (10.727). The intrinsic rate of increase (r_m) and the finite increase (λ) were the greatest on snap bean (0.205, 1.228, respectively), and the smallest on lima bean (0.125, 1.133, respectively), and the opposite was found for the doubling time (DT).

Table 2. Pre-, post-, and oviposition periods and adult longevity^a (day; mean \pm SE) of *Megalurothrips usitatus* on snap bean, cowpea, pea, and lima bean. Numbers in parentheses are live insects at that developmental stage.

Crop	Female								Male Longevity
	Longevity		Pre-oviposition		Oviposition		Post-oviposition		
	Sexual reproduction	Parthenogenesis	Sexual reproduction	Parthenogenesis	Sexual reproduction	Parthenogenesis	Sexual reproduction	Parthenogenesis	
Snap bean	15.63 \pm 0.83 a (27)	20.61 \pm 1.29 a (28)	1.03 \pm 0.17 bc (27)	1.39 \pm 0.09 a (28)	13.19 \pm 0.80 a (27)	18.11 \pm 1.19 a (28)	1.59 \pm 0.30 a (27)	1.18 \pm 0.21 b (28)	14.67 \pm 0.7 a (30)
Cowpea	14.48 \pm 0.67 ab (30)	15.08 \pm 0.66 b (24)	0.77 \pm 0.21 c (30)	1.46 \pm 0.15 a (24)	11.87 \pm 0.39 ab (30)	12.13 \pm 0.60 b (24)	1.67 \pm 0.15 a (30)	1.50 \pm 0.15 b (24)	7.73 \pm 0.45 b (30)
Pea	14.13 \pm 0.57 ab (25)	16.40 \pm 0.67 b (25)	1.36 \pm 0.17 ab (25)	1.36 \pm 0.11 a (25)	11.60 \pm 0.62 ab (25)	12.64 \pm 0.61 b (25)	1.44 \pm 0.22 a (25)	2.40 \pm 0.20 a (25)	7.15 \pm 0.66 b (27)
Lima bean	13.83 \pm 0.43 b (24)	15.63 \pm 0.64 b (30)	1.75 \pm 0.16 a (24)	1.63 \pm 0.18 a (30)	10.63 \pm 0.49 b (24)	11.87 \pm 0.56 b (30)	1.83 \pm 0.25 a (24)	2.87 \pm 0.34 a (30)	6.42 \pm 0.54 b (24)

^aMean values within the same column followed by different letters are significantly different by Tukey's multiple range test ($P < 0.05$).

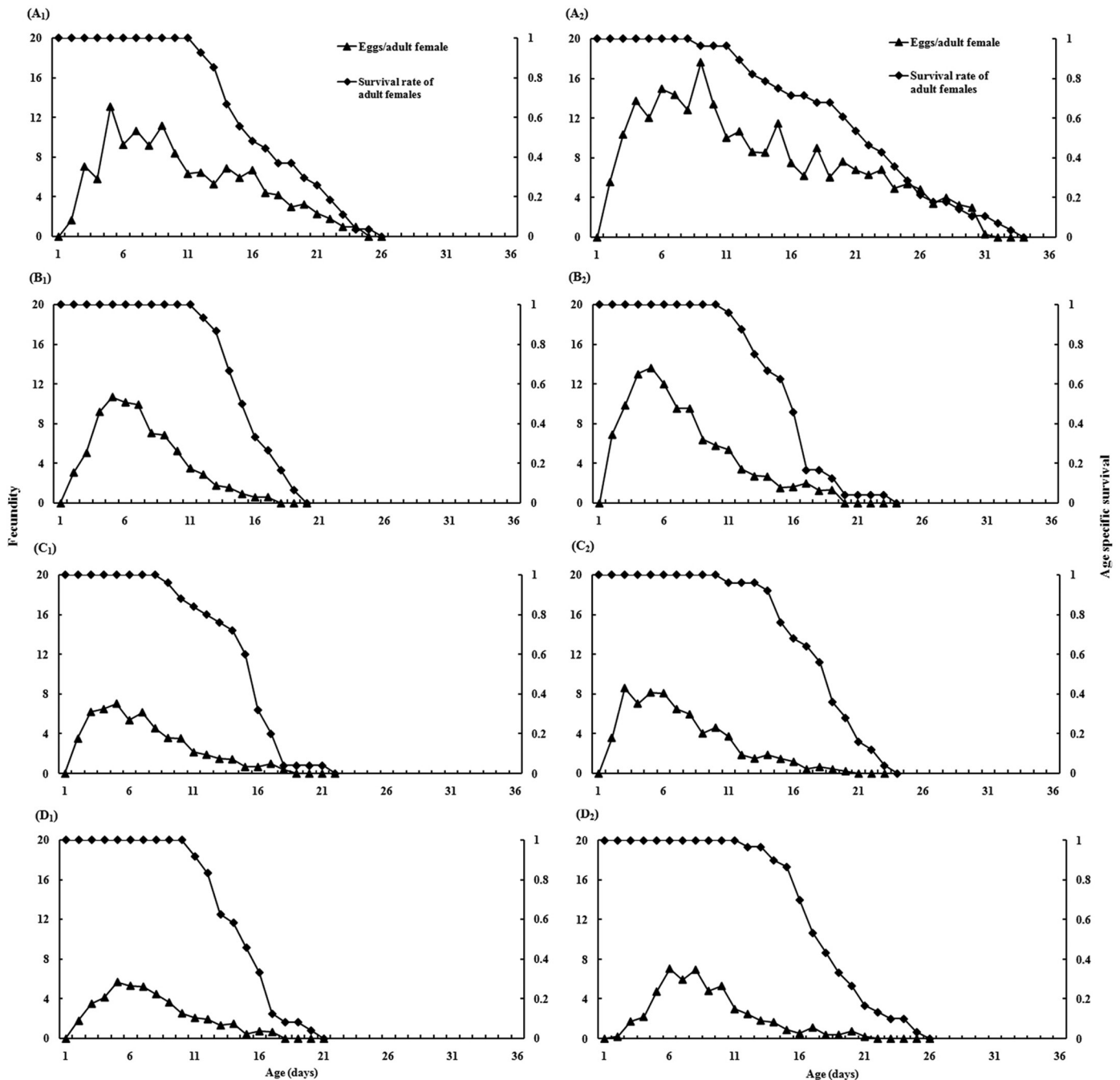


Fig. 2. Fecundity and survivorship of adult females of *Megalurothrips usitatus* on different leguminous crops: (A) snap bean, (B) cowpea, (C) pea, and (D) lima bean. The left column represents the sexual reproduction and the right column represents the parthenogenesis of *M. usitatus*.

Discussion

Biological attributes of thrips are closely associated with the quality of their host plants (Brødsgaard 1987; Brodbeck et al. 2002). Biological attributes include growth, development, survivorship, longevity, feeding and reproduction on different plant species (Scott Brown et al. 2002). A fast development rate and a large fecundity of insects on a host plant indicate that it is well suited as a host plant (van Lenteren & Noldus 1990). In this study, we investigated the life attributes of *M. usitatus* thrips on 4 leguminous crops. All of these species can be used to rear *M. usitatus* throughout its entire life cycle. However, the differences in the biological attributes of *M. usitatus* on 4 leguminous

species were significant and consistent, indicating that these plants differ in suitability as hosts of *M. usitatus*. The development times of *M. usitatus* immatures varied from 9.4 to 11.6 d on these 4 host plant species. The shortest development time was found on snap bean, and the longest on lima bean. The development times of immature stages of *M. usitatus* on soybean foliage and flowers at various temperatures were reported to be in the range of 9.0–21.7 d (Chang 1987). The reduced development time of *M. usitatus* on suitable food was mainly due to the rapid development of the larval stages, but the non-feeding prepupal and pupal stages also experienced reduced developmental times (Table 1). Similar results were reported for *Frankliniella occidentalis* (Hulshof et al. 2003; Zhang et al. 2007). Our results indicated that

the survivorship of immature stages was greatest on snap bean (Fig. 1). Adult longevity of *M. usitatus* was strongly dependent on the quality of food. In the present study, the shortest female longevities when reproducing either sexually or parthenogenetically were 13.83 or 15.63 d, respectively, on lima bean, whereas the longest female longevities were 15.63 or 20.61 d, respectively, on snap bean. Similar results were also obtained on the male longevities, although females lived longer than males (Table 2). Comparable longevity data for *F. occidentalis* on bean plants (pods) were 27.88 d (Zhi et al. 2005), 24.45 d (Gerin et al. 1994) and 10.8 d (Brødsgaard 1994). Our results showed the fecundity of *M. usitatus* was the least when the females were reared as larvae on lima bean with sexual reproduction (42.17 ± 2.99 eggs/female) and parthenogenesis (49.50 ± 3.90 eggs/female) (Table 3); corresponding fecundities were much greater than on soybean (Chang 1987). These differences between our observations and the previous findings by other researchers could be associated with the host plant species. In general, the shortest development time of immature stages, and greatest survivorship of immatures, adult longevity, and fecundity were found on snap bean. In contrast, the corresponding values on lima bean were the smallest. Suitabilities of host plant species for development and adult reproduction of *M. usitatus* in a decreasing order were: snap bean > cowpea > pea > lima bean.

Adult female thrips of *M. usitatus* have a rather opportunistic way of reproduction. They can reproduce both sexually and by parthenogenetically. In this study, thrips reproducing by parthenogenesis performed better than those reproducing sexually; those reproducing parthenogenetically had longer longevity and oviposition periods, and greater fecundities (Tables 2 and 3). Possibly, this can be attributed to the greater need for energy associated with mating behavior. Parthenogenesis allows insect species to sustain survival and reproduction at low densities.

The intrinsic rate of increase (r_m) is a reflection of several factors, including fecundity, survival, and generation time. The intrinsic rate of increase adequately summarizes the physiological qualities of an animal in relation to its capacity to increase (Fathi et al. 2011). Therefore, it is the most appropriate index for evaluating the performance of insects on different host plants, as well as for assessing host plant resistance (Smith 1989; Carey 1993; Southwood & Henderson 2000; Murai 2001). A significant difference was found in the intrinsic rates of natural increase of *M. usitatus* on different host plants in this study. The smallest and greatest r_m values were obtained on lima bean and snap bean (0.125 and 0.205), respectively (Table 4). In contrast, the intrinsic rate of increase (r_m) of *F. occidentalis* can be as large as 0.3 on cucumber (Gaum et al. 1994) but as small as 0.02 on peanuts (Lowry et al. 1992). The r_m values of *T. tabaci* can be as great as 0.296 on cucumber (Madadi et al. 2006) but as small as 0.085 on canola (Fathi et al. 2011). The differences between results of various studies could be

Table 3. Fecundities and sex ratios of *Megalurothrips usitatus* on snap bean, cowpea, pea, and lima bean. Numbers in parentheses are number of live insects from which data were collected.

Crops	Fecundity ^a (first instar larvae/female)(mean ± SE)		Sex ratio (females/total)
	Sexual reproduction	Parthenogenesis	
Snap bean	112.15 ± 11.98 a (27)	195.89 ± 19.24 a (28)	0.44
Cowpea	77.53 ± 3.61 b (30)	101.38 ± 6.93 b (24)	0.45
Pea	52.36 ± 2.06 c (25)	67.04 ± 4.39 c (26)	0.47
Lima bean	42.17 ± 2.99 c (24)	49.50 ± 3.90 c (30)	0.49

^aMean values within the same column followed by different letters are significantly different by Tukey's multiple range test ($P < 0.05$).

Table 4. Life history parameters of *Megalurothrips usitatus* on snap bean, cowpea, pea and lima bean.

Crop	R_0	r_m	λ	T	DT
Snap bean	40.333	0.205	1.228	18.012	2.277
Cowpea	20.909	0.181	1.199	16.775	2.402
Pea	19.029	0.171	1.186	17.230	2.461
Lima bean	10.727	0.125	1.133	18.995	2.773

attributed to the host plant/cultivar quality, as well as the species and/or strains of thrips.

The net reproductive rate (R_0) an host plant influence on insect population dynamics (Richard 1961; Morris & Fulton 1970; Varley & Gradwell 1970; Tsai & Wang 2001). In this study, the greatest R_0 value (40.333) was found on snap bean whereas the smallest (10.727) was on lima bean (Table 4).

Although *M. usitatus* prefer to live and feed on flowers, when these tissues are scarce they can feed on young leaves and pods of leguminous plants. This laboratory study indicated that pods of all 4 leguminous crops can be damaged by *M. usitatus*, and the order of suitability was obtained. Information of how leguminous host plant quality influences the life table parameters of *M. usitatus* can be useful in understanding the population dynamics in the field and for rearing the insect pests for future research in the laboratory.

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