Article

Temperature dependent development parameters and population life table of beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae)

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Abstract
Beet armyworm, *Spodoptera exigua* (Hübner), is an important insect pest fed on many crops. Temperature and host plant dependent development, survival, and population parameters of *S. exigua* were studied in present article. The results showed that the generation duration of *S. exigua* at temperatures 20, 25, 27, 30, and 35℃ were 37.61, 30.78, 22.40, 18.57, and 13.74 days, respectively. *S. exigua* could not survive at 38℃. The generation duration of *S. exigua*, feeding on *Lactuca sativa*, *Lactuca Sativa* L., *Raphanus sativus* L., and *Allium fistulosum* at 27℃, were 18.86, 20.10, 22.67, and 22.50 days respectively. And the generation survivorship was 30.91, 29.00, 22.00, and 27.50% respectively, far less than observed 81.91% feeding on artificial diet. *S. exigua* feeding on *L. sativa* showed the highest net reproduction rate (216.29), intrinsic rate for increase (0.34), population trend index (76.59), finite rate for increase (1.33), and fecundity (606.5 eggs), while these values were the lowest when it fed on *A. fistulosum*. Relationship between development rate and temperature was fitted with three models, the linear model, Logistic model and Wang model, and Wang model produced the best fitting goodness. Wang model showed that for the egg, the 1st-5th instar larvae, pupa and adult of *S. exigua*, the upper limit temperatures for development are 45, 44.5, 44.4, 40.3, 43.6, 38.9, 38, and 38 ℃, resepctively; the lower limit temperatures for development are 7.5, 7.2, 13.4, 7.3, 6.6, 5.3, 5.6, and 5.6 ℃, respectively, and the optimum temperatures for development are 21.9, 28.9, 25.5, 24.5, 26, 31.6, 30.6, and 29.1 ℃, respectively. The upper limit, lower limit and optimum temperatures for development of the entire generation are 38, 5.7 and 30 ℃, resepctively.

Keywords *Spodoptera exigua*; life table; population parameters; temperature; development; host plants.

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1 Introduction

Spodoptera exigua (Hübner) (Lepidoptera: Noctuidae) possesses wide distribution, multi-host plants, strong migration ability, and high temperature suitability. It feeds on 170 species, involving 35 families of plants, and injures vegetables, cotton, tobacco, corn, peanuts, and sugar beet, etc (Feng et al., 1995; Liu et al., 1998; Luo and Cao, 2000; Greenberg et al., 2001; Karimi-Malati et al., 2014).

S. exigua larvae have generally five instars, sometimes six instars (Ali and Gaylor, 1992). The first instar larvae has a positive phototaxis, the second instar larvae has a weak negative phototaxis. The light intensity don't impact the third and fourth instar larvae distribution, and the fifth instar larvae have the strong negative phototaxis (Griswold, 1985). Early larve of *S. exigua* injure host plants mainly in group but they spread after the third instar larvae. Larvae feed mostly at night. Starting from the fourth instar, larvae's food intake increase. The fourth and fifth instar larvae comsump 80-90% of total food at the larvae stage. The older instar larvae pupate in the soil (Fey, 1978). Female moths can quickly lay eggs after mating. The female moth can lays 713±154 eggs for 4.8±1.5 days (Wakamura, 1990).

Research showed that larvae's duration at 20, 25, and 30 ℃ were 32.3, 17.3, and 10.5 days, respectively. The lower limit temperatures for development of egg, larva, and pupa were 13.2, 15.4, and 15.4℃, and the effective accumulated temperature were 37.2, 155.8, 78.5 day-degrees, respectively (Lee, 1991). Yin revealed that the lower limit temperatures for development of egg, larva, pupa were 10.99, 10.93, and 12.19 ℃ at the room temperature and the effective accumulated temperature were 42.55, 243.32, and 105.73 day-degrees, respectively (Yin, 1994).

Ali and Gaylor (1992) exploited the effects of temperature and host plants on the development of *S. exigua*. The results showed that between 15~36 ℃, its development had linear growth relationship, and a high temperature exceeding 36 ℃ could restrain its development.

Food and nutrition has a great impact on the larval development and adult reproduction. Ali and Gaylor (1992) found that pupal weight closely related to nutrition. When feeding with artificial food, the body weight of *S. exigua* pupa was greater than that feeding with plant tissue. Chen et al. (1999) and Jiang et al. (1999) demonstrated that the development duration, pupal weight, fecundity and flight ability of *S. exigua* larva, pupa and adult were different when fed on different host plants.

Life table is an important research method for theoretical population dynamics and population parameters of insects. At present, life tables have been widely used to forecast pest population, evaluate various control measures, and to develop populations dynamic models (Ding, 1994).

This study aims to explore temperature and host plant dependent development, survival, and population parameters of *S. exigua*, in order to obtain some population parameters for prediction and control of the pest.

2 Materials and Methods

2.1 Materials

S. exigua was collected from Guangzhou Institute of Vegetable. Indoor feeding with artificial formula and host plants was conducted.

Artificial formula: casein 2g, soybean meal 10g, yeast 4g, wheat bran 6g, sorbic acid 0.2g, Nipagin 0.2g, ascorbic acid 0.4g, cholesterol 0.1g, chloride 0.08g, trace nutrients I 2500IU , trace nutrients Ⅱ 1000 IU, micro-nutrients Ⅲ, micro-nutrients IV 0.5mg, micro-nutrients V 3mg, agar 1.6g, water 100m1.

Host plants: *Raphanus sativus* L., *Allium fistulosum*, *Lactuca sativa*, *Lactuca Sativa* L., were cultivated under natural conditions at experimental garden without any chemicals.

2.2 Methods

2.2.1 Rearing conditions : Insects were reared in artificial climate boxes with controlled temperatures, the temperature fluctuation was ± 1 ℃. Fluorescent controlled light was used. Light periodicity is L: D = 12:12, and relative humudity is 75% ~ 85%.

2.2.2 Disinfection measures: In order to prevent disease, climate boxes were disinfected two hours before experiments using ultraviolet light or vaporization of 10 ml of 36.5% solution of formaldehyde. Appliances (tubes, forceps, feeding kit, etc.) were disinfected 30 minutes using high-temperature autoclave sterilization pan. Experimental room was regularly disinfected using 0.2% of sodium hypochlorite disinfectant.

2.2.3 Feeding methods

2.2.3.1 Eggs disinfection: Before the eggs hatched, add the eggs in the 5% formaldehyde solution for disinfection for 15 min, and then clean, dry them with pure water. After the counting, put into a circular plastic box (13 cm × 4 cm, each with 40 to 100 eggs), and thereafter count the number of hatching eggs.

2.2.3.2 Larvae culture: Early larvae are still fed in circular plastic boxes (13 cm × 4 cm), until the third instar larvae. Distribute larvae in two boxes for rearing until larvae nearly pupate. Transfer mature larvae to pupation boxes. Record larvae number, mortality, larval duration and pupation rate.

2.2.3.3 Adults: In the pre-pupae period, remove the pupae from the sand, and identify male and female. Emerged female and male moths were paired. Add every pair of moths into a glass with diameter of 7 cm and height of 10 cm, and add 15% of honey supplements in the glass. The daily egg mass took out of the glass, Calculate the number of laid eggs every day. Record life expectancy of adults and hatching rate of eggs.

2.2.4 Experimental methods

2.2.4.1 Experiment: set six rearing temperatures, 20, 25, 27, 30, 35, and 38 ℃, and set each temperature with 3 replicates.

2.2.4.2 Experiment: at 27 ℃, use four host plants rearing *S. exigua* larvae, set each host plant with 2 replicates.

2.2.5 Analysis Methods

2.2.5.1 Life table analysis

Calculate the net reproductive rate (R_0), intrinsic rate of increase (r_m), finite increase rate (λ), mean generation time (T), population doubling time (DT) and population trend index (I) (Birch et al., 1948; Wu et al., 1980)

$$R_0=\sum l_x m_x \quad (1)$$

$$T=\sum x l_x m_x / \sum l_x m_x \quad (2)$$

$$r_m=\ln R_0/T \quad (3)$$

$$\lambda=e^{rm} \quad (4)$$

$$DT=\ln 2/r_m \quad (5)$$

$$I=S*P_{♀}*E \quad (6)$$

where l_x: age-specific survival rate, m_x: age-specific fertility, S: generations survival rate, $P_{♀}$: male ratio, and E: reproduction rate.

2.2.5.2 Temperature dependent development model of *S. exigua*

(1) Linear degree-day model

$$V(t)= t/K-C/K \quad (7)$$

where t: experimental temperature (℃), $V(t)$: development rate, K: effective accumulated temperature (day degrees), and C: lower limit temperature for development (℃).

(2) Logistic model

$$V(t)=K/(1+ \exp(a-bt)) \quad (8)$$

where t: experimental temperature (℃), $V(t)$: development rate, K, a, and b are parameters, and K is the potentially maximum development rate.

(3) Wang model (Wang et al., 1982)

$$V(t)=(K / [1 + \exp(-r (t-T_O))]*[1-\exp(-(t-T_L) / \delta)]*[1-\exp(-(T_H-t) / \delta)] \quad (9)$$

where t is the temperature (℃), $V(t)$: development rate, K: about 2-fold of the optimal development rate, r: growth rate of development with temperature, T_O: the optimum developmental temperature, T_L: lower limit temperature for development, T_H: upper limit temperature for development, and δ: the parameter for tolerance of extreme temperatures.

3 Results and Discussions

3.1 Effects of temperature on development and population parameters of *S. exigua*

3.1.1 Effects of temperature on development duration and survivorship

At different temperatures, the development duration for different stages and entire generation of *S. exigua* are presented in Table 1. Results show that at 20~35 ℃, the development duration of *S. exigua* reduces with the temperature. At 20 ℃, the egg, the different larval stages, the pupa and the entire generation have the longest development duration, followed by that at 25, 27 and 30 ℃. At 35 ℃ it has the shortest development duration. When the temperature exceeds 35 ℃, the development duration begins to increase. If the temperature reaches 38 ℃, *S. exigua* can not complete the whole generation. It is slightly different the results of Yin et al. (1994) that the older larvae could not pupate after four hours' treatment at 40 ℃.

Table 1 Development duration of each stages of *S. exigua* at six temperatures.

Temp.	Egg	1st-instar	2nd-instar	3rd-instar	4th-instar	5th-instar	Pupa	Adult	Generation
20℃	3.20± 0.07a	2.83± 0.08a	3.06± 0.13a	3.48± 0.17a	3.64± 0.18a	4.54± 0.26a	7.68± 0.07a	9.18± 0.34a	37.61± 0.31a
25℃	1.04± 0.03b	1.94± 0.04b	1.69± 0.13b	1.55± 0.05b	2.08± 0.13b	3.08± 0.05b	6.63± 0.11b	12.76± 0.71b	30.78± 0.78b
27℃	0.93± 0.02c	1.96± 0.01b	1.50± 0.01b	1.05± 0.06c	1.35± 0.16c	1.91± 0.04c	5.64± 0.14c	8.06± 0.05c	22.40± 0.01c
30℃	0.93± 0.03c	1.84± 0.04b	1.24± 0.01c	1.02± 0.06c	1.08± 0.01c	1.73± 0.03d	3.99± 0.07d	6.75± 0.04d	18.57± 0.02d
35℃	0.76± 0.01d	1.10± 0.14c	1.16± 0.04c	1.08± 0.11c	1.12± 0.08c	1.53± 0.07e	3.12± 0.04e	3.85± 0.22e	13.74± 0.20e
38℃	1.00± 0.01e	1.32± 0.04c	1.28± 0.02c	1.80± 0.02d	1.25± 0.04c	3.49± 0.03f	—	—	—

The data in the table are presented as Mean ± *SD* and those in the same column followed by different letters are significantly different by Duncan's multiple range test (p<0.05). It is the same for the following tables.

At 20, 25, 27, 30 and 35 ℃, the generation's development duration are 37.61, 30.78, 22.40, 18.57 and 13.74 days, respectively, similar to the previous report (Han et al., 2003). But the larva's development duration is significantly shorter than previous findings (Lee, 1991; Han et al., 2003).

Development duration of the entire generation (*D*) follows the relationship, *D*=-1.665*t*+70.24, where *t* is temperature.

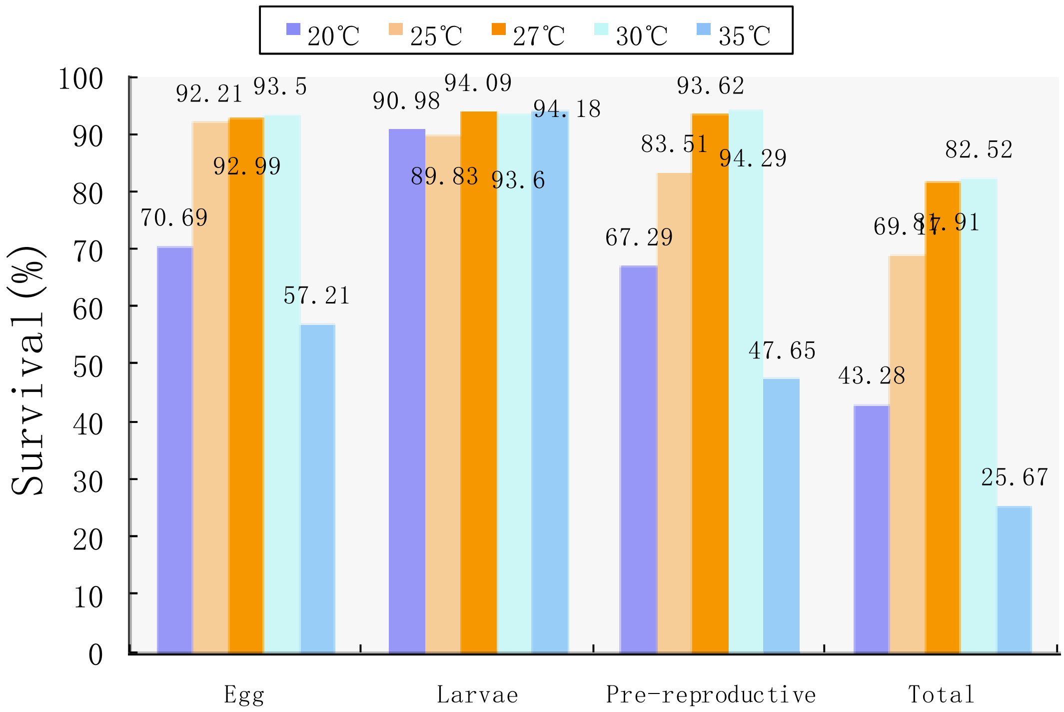

Fig. 1 Survivorship of different stages of *S. exigua* at five temperatures.

The different developmental stages' survivorship of *S. exigua* at different temperatures are shown in Fig. 1. The results show that the generation's survivorship of *S. exigua* increases with temperature within 20~35 ℃; at 30 ℃ it has the maximum survivorship of 82.52%, and then decreases with the increase of temperature, then reaches 0 at 38 ℃. Ma et al. (1999) had a similar result that at 30 ℃ the insect's entire generation has the maximum survival rate.

The results show that with the maximum survivorship, egg hatching rate reaches 93.50~92.21%, larval survivorship reaches 94.09~89.83%, and pre-reproductive survivorship reaches 83.51~94.29% within 25~30 ℃. This is a little different from the findings of Xu et al. (1999), that the temperature range 26~28 ℃ exibited the maximum survivorship.

Generation's survivorship follows the relationship, S=-0.5499t^2+29.47t-299.5, where t is temperature.

3.1.2 Effects of temperature on population life parameters

In general, the average life expectancy decreases with the temperature. Net reproductive rate, intrinsic rate of increase, finite increase rate, population trend index and egg production increase with the increasing temperature, but these parameters decrease with the increasing temperature when the temperature exceeds 30 ℃ or so. At 27~30 ℃, population life parameters of *S. exigua* have better performance than at other temperatures (Table 2).

Table 2 Fecundity and population parameters of *S. exigua* at five temperatures.

Population parameters	20℃	25℃	27℃	30℃	35℃
T	36.4695	26.4249	21.8422	18.5007	14.5127
r_m	0.1248	0.238	0.2844	0.3406	0.2233
R_0	94.8982	538.847	498.3079	545.175	25.527
λ	1.1329	1.2687	1.3289	1.4058	1.2501
I	34.9755	236.4299	245.1225	260.0543	14.3167
DT	5.555	2.9126	2.4378	2.0353	3.105
E	164.95	746.8333	602.25	664.7	122.5

R_0: net reproductive rate, r_m: intrinsic rate of increase, λ: finite increase rate, T: mean generation time, DT : population doubling time, I: population trend index, E: fecundity of the female adult (eggs/female).

The population parameters and temperature have the following relationships:

T= 112.3-5.11t+0.0661t^2 R=0.987

r_m= -1.504+0.1228t-0.0021t^2 R=0.957

R_0= -6058+485.7t-8.903t^2 R=0.987

λ=-0.9003+0.1533t-0.0026t^2 R=0.946

I= -2907+231.3t-4.22t^2 R=0.991

DT= 34.28-2.163t+0.0363t^2 R=0.999

E= -6892+557.8t-10.22t^2 R=0.970

3.1.3 Temperature dependent development models

The results show that Wang model is the best model for describing temperature dependent development of *S. exigua*.

Based on linear day-degree model, the lower limit temperatures for development are 6.54, 8.01, 5.15, 10.57, and 9.42 ℃, respectively, and the effective accumulated temperature are 23.62, 35.79, 34.49, 22.88, and 29.13, respectively, for the egg and the 1st-4th instar larvae (Table 3).

Logistic model fits better than linear degree-day model and *K* values for the egg and the 1st-4th instar larvae are 1.16, 1.12, 0.86, 0.85, and 0.90.

Table 3 Model parameters of temperature depedent development of *S. exigua*, corresponding to eq. 7, 8, 9.

Stages	Linear degree-day model				Logistic model				
	C	*K*	*R*	*SSE*	*K*	*a*	*b*	*R*	*SSE*
Egg	6.542	23.62	0.7810	0.6524	1.1630	11.03	0.5020	0.9609	0.1283
1st-instar	8.014	35.79	0.8847	0.1328	1.1150	3.085	0.1130	0.8889	0.1284
2nd-instar	5.152	34.49	0.9005	0.1036	0.8508	6.046	0.2770	0.9813	0.0203
3rd-instar	10.57	22.88	0.8482	0.7386	0.8532	10.88	0.5058	0.9756	0.3248
4th-instar	9.416	29.13	0.8513	0.2547	0.9025	7.609	0.3267	0.9441	0.1007
5th-instar	-0.742	69.20	0.5329	0.2998	0.5311	7.319	0.3391	0.7057	0.2102
Pupa	-61.80	510.3	0.1233	0.1415	0.2003	5.560	0.3019	0.2787	0.1325
Adult	-29.77	464.4	0.1668	0.0922	0.1502	3.009	0.1744	0.2239	0.0901
Generation	0.1792	709.1	0.0005	0.0081	0.0466	6.488	0.3299	0.3381	0.0071

Stages	Wang model								
	K	*r*	T_O	T_L	T_H	δ	*R*	*SSE*	*n*	*p*

Egg	1.163	0.5020	21.98	7.500	45.00	2.015	0.9609	0.1283	15	95
1st-instar	1.311	0.1164	28.96	7.236	44.47	4.531	0.8889	0.1210	15	95
2nd-instar	1.453	0.1236	25.47	13.36	44.35	5.845	0.9934	0.0072	15	99
3rd-instar	1.357	0.2865	24.53	7.257	40.27	4.183	0.9756	0.0495	15	95
4th-instar	1.419	0.2337	26.03	6.572	43.66	6.349	0.9704	0.0542	15	95
5th-instar	1.405	0.1521	31.56	5.261	38.97	2.936	0.9770	0.0190	15	95
Pupa	0.5737	0.1567	30.61	5.617	38.03	2.000	0.9663	0.0095	15	95
Adult	0.3285	0.1552	29.05	5.622	38.00	2.596	0.9227	0.0141	15	95
Generation	0.115	0.1481	30.00	5.655	38.00	1.114	0.9866	0.0001	15	95

SSE: the residual sum of squares, *R*: correlation coefficient, and *p*: confidence level (%).

Wang model demonstrates that for the egg, the 1st-5th instar larvae, pupa and adult, the upper limit temperatures for development are 45, 44.5, 44.4, 40.3, 43.6, 38.9, 38, and 38 ℃, resepctively; the lower limit temperatures for development are 7.5, 7.2, 13.4, 7.3, 6.6, 5.3, 5.6, and 5.6 ℃, respectively; the optimum temperatures for development are 21.9, 28.9, 25.5, 24.5, 26, 31.6, 30.6, and 29.1 ℃, respectively. The upper limit, lower limit and optimum temperatures for development of entire generation are 38, 5.7 and 30 ℃, resepctively (Table 3).

3.2 Effects of host plants on development and population parameters of *S. exigua*

3.2.1 Effects of host plants on development duration and survivorship

At 27 ℃, the development duration and survivorship of different stages of *S. exigua* fed on *Lactuca sativa*, *Lactuca Sativa L.*, *Raphanus sativus L.*, *Allium fistulosum* and artificial diet are presented in Table 4 and Fig. 2 respectively.

Table 4 Development duration of *S. exigua* fed with different host plants.

Host plants	Development duration（days）								
	Egg	1st-instar	2nd-instar	3rd-instar	4th-instar	5th-instar	Pupa	Adult	Generation
Lactuca sativa	0.95± 0.01a	1.67± 0.01a	1.89± 0.04a	1.55± 0.06a	1.79± 0.02a	2.80± 0.01a	4.69± 0.11a	6.19± 0.12a	18.86± 0.13a
Lactuca Sativa L.	0.94± 0.02a	1.60± 0.03b	1.77± 0.01b	1.67± 0.04b	1.79± 0.01a	2.93± 0.01b	5.20± 0.01b	5.20± 0.02b	20.10± 0.03b
Raphanus sativus L.	0.91± 0.00a	1.68± 0.01a	1.77± 0.00b	2.04± 0.03c	2.73± 0.06b	3.97± 0.01c	5.60± 0.05c	5.46± 0.01c	21.50± 0.00c
Allium fistulosum	0.91± 0.00a	1.66± 0.04ab	1.88± 0.09a	2.02± 0.03c	2.33± 0.03c	4.20± 0.09d	6.42± 0.02d	5.92± 0.08d	22.67± 0.13d
Artificial diet	0.93± 0.02a	1.96± 0.01d	1.50± 0.00d	1.05± 0.06d	1.35± 0.12d	1.91± 0.03e	5.64± 0.14c	8.06± 0.05e	22.40± 0.01d

The results show that feeding on *Lactuca sativa*, the insect has the shortest generation duration of 18.86 days, followed by *Lactuca Sativa L.* (20.10 days). Feeding on *Raphanus sativus L.*, *Allium fistulosum*, the insect’s generation duration are 22.50 days and 22.67 days, longer than that feeding on the artificial diet. There is not significant difference between generation duration feeding on *Allium fistulosum* and artificial diet.

Feeding on *Lactuca Sativa L*, and *Raphanus sativus L.* the larvaal development duration are 9.76 days and 12.19 days, but Song (2008) found that the larval development duration were 11.53 days and 12.43 days respectively.

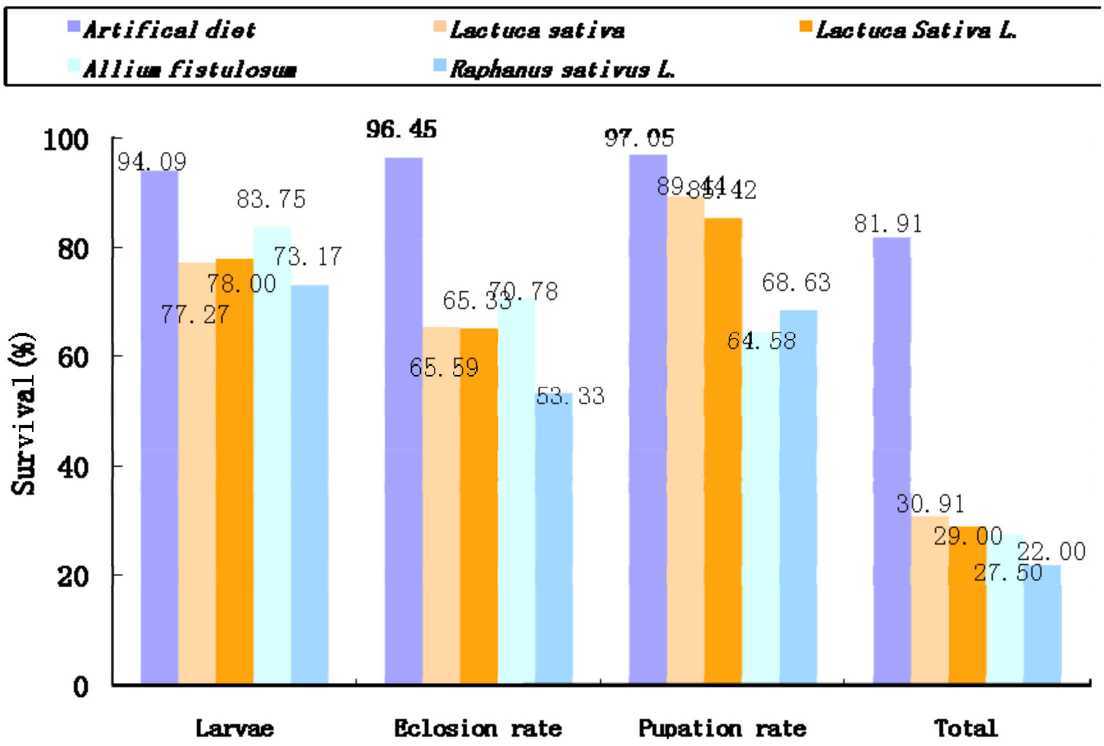

Fig. 2 Survivorship of *S. exigua* fed with different host plants.

Fig. 2 show that survivorship of *S. exigua* feeding on artificial diet are significantly higher than host plants, followed by *Lactuca sativa*, *Lactuca Sativa L.*, *Allium fistulosum*, and *Raphanus sativus L.*

3.2.2 Effects of host plants on population life parameters

From Table 5, it can be found that in the four host plants, *Lactuca sativa* performs the best in fecundity, net reproductive rate, intrinsic rate of increase, finite increase rate, average life expectancy of the population, and population doubling time of *S. exigua*, followed by *Lactuca Sativa L.*, *Raphanus sativus L.*, and *Allium fistulosum*.

Table 5 Effects of host plants on population life parameters of *S. exigua*.

Population life parameters	*Lactuca sativa*	*Lactuca Sativa L.*	*Raphanus sativus L.*	*Allium fistulosum*
T	18.665	19.3829	20.3644	22.5591
r_m	0.2880	0.2691	0.1997	0.1701
R_0	216.2893	184.1196	58.5017	46.4072
λ	1.3338	1.3088	1.2211	1.1855
I	76.5963	73.1839	36.2677	24.0006
DT	2.4070	2.5760	3.4713	4.0748
E	606.50	506.95	206.65	169.30

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