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Climate Change

Demography and Population Projection of Flea Beetle, *Agasicles hygrophila* (Coleoptera: Chrysomelidae), Fed on Alligator Weed Under Elevated CO_2

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Abstract

The flea beetle, *Agasicles hygrophila* Selman and Vogt, was introduced into China in 1987. For a more comprehensive understanding of the effect of elevated CO_2 concentration on the population dynamics, we collected the life table data of the flea beetle, *A. hygrophila*, at two different CO_2 concentration conditions, i.e., ambient (420 μl/liter) and elevated (750 μl/liter). The raw data were analyzed using the age-stage, two-sex life table theory. At 750 μl/liter CO_2, shorter developmental durations of the egg, first instar, and pupa were observed, while the duration of the third instar and the total developmental duration of the larva were prolonged. The generation length of *A. hygrophila* was significantly shortened at the higher concentration. It was observed that the intrinsic rate of increase (r), finite rate (λ), and net reproduction rate (R_0) were higher and the mean generation time (T) was shorter at 750 μl/liter compared with that at 420 μl/liter. The bootstrap techniques were adopted to estimate the variances and standard errors of the developmental time, longevity, fecundity, and the population parameters. The bootstrap technique generated a normal distribution that was consistent with the central limit theorem and critical for following statistical analysis and comparison. Population projections based on age-stage, two-sex life tables could reveal the stage structure of *A. hygrophila* population and the leaf consumption capacity. Data collected in this study can potentially be used to evaluate the efficacy of *A. hygrophila* as a biological control agent of the alligator weed.

Key words: *Agasicles hygrophila*, elevated CO_2, life table, leaf consumption, population projection

Alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb (Amaranthaceae), originated in the Parana River region of South America (Maddox 1968, Vogt et al. 1979). It was introduced into China in the 1930 s, and was listed as one of the 16 most important invasive species in China (Ministry of Environmental Protection of the People's Republic of China, Chinese Academy of Sciences 2003). The flea beetle, *Agasicles hygrophila* Selman and Vogt, has been studied as a biological control agent against the alligator weed in the United States, Australia, New Zealand, and China (Spencer and Coulson 1976, Julien 1992, Julien et al. 1995, Guo et al. 2012). The flea beetle population was established in southern China after an accidental release in 1989 in Fuzhou, Fujian province, when *A. hygrophila* was accidentally introduced from South America (Wu 1997).

The average level of CO_2 has increased from ~280 μl/liter immediately before the Industrial Revolution to a daily average of 380 μl/liter in 2005 and is increasing at a rate of about 2 μl/liter per year. A value of 570 μl/liter atmospheric CO_2 is expected by the end of this century, and global levels of CO_2 are predicted to double (average of 770 μl/liter) by the year 2200 (Intergovernmental Panel on Climate Change [IPCC] 2007).

Plant chemistry can be strongly affected by elevated CO_2 concentrations. Elevated CO_2 may increase rates of photosynthesis, which could enhance plant growth, biomass accumulation, and plant size (Frenck et al. 2011, Klaiber et al. 2013a). Thus, these changes could directly impact plant–insect herbivore interactions (Agrell et al. 2006). So, the elevated CO_2 concentrations not only directly affect the physiology of plants but also affect phytophagous insects indirectly. Entomologists have recognized that elevated CO_2 influences the distribution, abundance, and performance of herbivorous insects (Lincoln et al. 1984, Fajer 1989). Guerenstein and

Hilderbrand (2008) reviewed the effect of CO_2 on insect life. Chen et al. (2005) showed that the body weight and growth rate of the cotton aphid, *Aphis gossypii* (Glover), were increased at higher CO_2 concentration. Yin et al. (2009), however, showed that elevated CO_2 had variable effects on the population parameters of *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae).

Most studies on elevated CO_2 have been focused on the growth, reproduction, or food consumption of specific stages (Wu et al. 2006, Sun et al. 2009, Huang et al. 2013, Klaiber et al. 2013b). Because studies focused on specific stages of a species do not reveal the overall effect on an insect population, the above studies contributed only limited knowledge to the consequences that elevated CO_2 has at the population level. In order to comprehensively understand the overall effect of an environmental factor on an insect population, it is necessary to detect its effect on the survival rate, developmental rate, and fecundity throughout their entire life span, i.e., the life table. Because the traditional female age-specific life table (Birch 1948, Carey 1993) ignores male individuals and cannot describe the stage differentiation, their application to two-sex populations will usually result in a number of problems (Huang and Chi 2012a). In the present research, the direct effects of elevated CO_2 (750 µl/liter) on the life table of the flea beetle, *A. hygrophila*, reared in a closed-dynamic CO_2 chamber were compared with the life table data of the untreated control group reared in ambient CO_2 (420 µl/liter). Data obtained from using the age-stage, two-sex life table (Chi and Liu 1985, Chi 1988) were then utilized to simulate the population growth of the flea beetle and its efficacy as a biological control agent against *A. philoxeroides*.

Materials and Methods

Insect Rearing

The initial culture of the flea beetle, *A. hygrophila*, was obtained from the Institute of Plant Protection, Fujian Academy of Agricultural Sciences (IPP, FAAS), China, and maintained in a phytotron under controlled conditions of 25 ± 1°C, 80 ± 5% relative humidity, and a photoperiod of 12:12 (L:D) h. The insects used in this experiment were reared in elevated CO_2 concentrations (750 ± 28.8 µl/liter) or at normal atmospheric concentrations (420 ± 20.1 µl/liter) in a closed-dynamic CO_2 chamber for one generation prior to the experiments.

Plant Growth Conditions

The host plant, alligator weed (*A. philoxeroides*), used in this experiment was collected from a field greenhouse at the IPP, FAAS. Plants were watered twice a week throughout the study to maintain soil moisture. Pest-free alligator weeds (20–30 cm in height, stem diameter 2–2.5 mm) with leaves intact and without flea beetle damage were used in the experiments.

Life Table Study

Newly emerged adults were paired and placed in separate plastic boxes (18 cm in length, 11 cm in width, and 7 cm in height). Eggs laid within a 24-h period were removed, placed in glass Petri dishes (11 cm in diameter) for life table studies, and kept in growth chambers. In total, 200 eggs were used for the life table study in each of the two CO_2 concentrations. The number and hatch rates of eggs were recorded daily. The first-instar larvae were individually transferred to separate glass Petri dishes (9 cm in diameter containing a filter paper moistened with water) provided with a fresh leaf of *A. philoxeroides*, and maintained through the third instar. The number of surviving larvae and the developmental stage were recorded, and the leaves replaced daily. At the end of the third instar, the larvae stopped feeding and were ready for pupation. A section of plant tip with three stem nodes (∼4–5 cm in length) without leaves was supplied for pupation. Each stem was inserted into a piece of floral foam soaked with water to avoid dehydration, placed into a plastic tube (2.5 cm in diameter, 12 cm in length), and covered with fine mesh net. The pupal duration and the number and sex of emerging adults were recorded daily.

As adults emerged, male and female beetles were paired and moved to a new glass container (5 cm in diameter, 8 cm in height) for oviposition. The fecundity and survival of the beetles were recorded for each individual until the deaths of all adults. If a beetle died earlier than its mate, another of the same sex was supplied from the mass-rearing colony. The data of these recruited individuals were excluded from analysis. Insects were kept separated in each of the growth chambers set at respective CO_2 concentration for the entire life table study period.

Life Table Data Analysis

The raw life history data for survival, longevity, and female daily fecundity of *A. hygrophila* individuals were analyzed using the TWOSEX-MSChart (Chi 2015) program, based on the age-stage, two-sex life table theory and the method described by Chi and Liu (1985) and Chi (1988). The TWOSEX-MSChart program is available at http://140.120.197.173/ecology/. The survival rate (s_{xj}; x = age, j = stage), which is the probability that a newly laid egg will survive to age x and stage j, and fecundity f_{xj}, which is the number of hatched eggs produced by a female adult at age x, were calculated. According to Chi and Liu (1985), the specific survival rate (l_x) is then calculated as:

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

where m is the number of stages. To take individuals of different stages at age x into account, the age-specific fecundity (m_x) is calculated as:

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

The total number of offspring that an individual can produce during its lifetime, i.e., the net reproductive rate (R_0), is calculated as:

$$R_0 = \sum_{x=0}^{\infty} l_x m_x \tag{3}$$

The intrinsic rate of increase (r) using the Lotka–Euler equation with age indexed from zero (Goodman 1982) is calculated as:

$$\sum_{x=0}^{\infty} e^{-r(x+1)} l_x m_x = 1 \tag{4}$$

The mean generation time (T) represents the period that a population requires to increase to R_0-fold of its size as time approaches infinity and the population growth rate settles down to the intrinsic rate and finite rate. Mean generation time is calculated as:

$$T = \frac{\ln R_0}{r} \tag{5}$$

According to Chi and Su (2006), the age-stage-specific life expectancy (e_{xj}), i.e., the time that an individual of age x and stage j is expected to live, is calculated as:

$$e_{xj} = \sum_{i=x}^{\infty}\sum_{y=j}^{m} s'_{iy} \tag{6}$$

where s'_{iy} is the probability that an individual of age x and stage j will survive to age i and stage y. Fisher (1930) defined the reproductive value as the contribution of individuals of age x and stage y to the future population. According to Huang and Chi (2011) and Tuan et al. (2014), the reproductive value in the age-stage, two-sex life table is calculated as:

$$v_{xj} = \frac{e^{r(x+1)}}{s_{xj}}\sum_{i=x}^{\infty} e^{-r(i+1)}\sum_{y=j}^{m} s'_{iy}f_{iy} \tag{7}$$

The standard errors of developmental time, longevity, fecundity, and population parameters were calculated by using the bootstrap method with 200,000 bootstrap replicates (Efron and Tibshirani 1993, Huang and Chi 2012b). Differences between treatments were compared using the paired bootstrap test (Efron and Tibshirani 1993, Smucker et al. 2007, Polat Akköprü et al. 2015).

Population Projection

To reveal the dynamic change of stage structure and leaf consumption of the populations of *A. hygrophila* under different CO_2 concentrations, we projected the population growth and leaf consumption based on the age-stage, two-sex life table (Chi and Liu 1985, Chi 1990) by using the computer program TIMING-MSChart (Chi 2015). At 420 µl/liter CO_2, the daily mean leaf consumption of the first instar, second instar, third instar, and adult were 3.12, 13.07, 41.96, and 49.95 mm^2 per insect, respectively, while they were 4.93, 10.65, 37.68, and 37.83 mm^2 per insect, respectively, at 750 µl/liter CO_2 (unpublished data of authors). For comparative purpose, the same initial population of 10 newborn eggs was used for the simulation at different CO_2 concentrations. The data file for TIMING-MSChart was generated by the TWOSEX-MSChart program. Because the age-stage, two-sex life table is capable of describing the stage differentiation during population growth, we calculated the increase rate of stage j from time t to $t+1$ using the common logarithm according to Akca et al. (2015) as:

$$\varphi_{j,t} = \frac{\log\,(\mathrm{n}_{j,t+1}+1)}{\log\,(n_{j,t}+1)} \tag{8}$$

where $n_{j,t}$ is the number of individuals in stage j at time t. According to Akca et al. (2015), we also used the natural logarithm to calculate the increase rate of stage j from time t to $t+1$ as:

$$\mathrm{r}_{j,t} = \ln\left(\frac{n_{j,t+1}+1}{n_{j,t}+1}\right) = \ln(n_{j,t+1}+1) - \ln(n_{j,t}+1) \tag{9}$$

When the individual number of a stage is 0 ($n_{j,t}=0$ or $n_{j,t}+1=0$), logarithmic transformation is impossible. Therefore, we used $n_{j,t+1}$ and $n_{j,t+1}+1$ in the calculation of $\o_{j,t}$ and $r_{j,t}$ (Akca et al. 2015).

Results

Development Time and Fecundity

The developmental times of the egg and the first instar in 420 µl/liter CO_2 were significantly longer than those in 750 µl/liter CO_2, while the developmental time of the third instar in 420 µl/liter CO_2 was shorter than that in 750 µl/liter CO_2 (Table 1). However, the total developmental time for the preadult stages was 24.13 d in 420 µl/liter CO_2, which was significantly longer than the 22.22 d in 750 µl/liter CO_2. The total longevities of both sexes in 420 µl/liter CO_2 were, however, significantly longer than those in 750 µl/liter CO_2. When the longevities of all individuals were used to calculate the mean longevity, there was no significant difference between the two treatments.

There was also no significant difference in adult preoviposition period (APOP) between the two CO_2 concentrations. There was, however, significant difference in the total preoviposition period (TPOP) between 420 and 750 µl/liter CO_2. The mean fecundity of 117.60 eggs per female in 750 µl/liter CO_2 was not significantly different than the 93.67 eggs produced in 420 µl/liter CO_2.

The standard errors of developmental time, longevity, and fecundity were estimated using the bootstrap method. As Polat Akköprü et al. (2015) observed, the general statistical procedure uses all individuals in a cohort to calculate the mean, variance, and standard errors, which generates a nonnormal frequency distribution (Fig. 1),

Table 1. Developmental time, longevity, APOP, TPOP, and fecundity (mean ± SE) of *A. hygrophila* under different CO_2 conditions

Parameter	Stage	420 µl/liter		750 µl/liter		*P*
		n	Mean ± SE	*n*	Mean ± SE	
Developmental time (d)	Egg	200	5.59 ± 0.03a	171	4.87 ± 0.03b	0.0000
	L1	169	3.51 ± 0.05a	159	3.22 ± 0.06b	0.0003
	L2	156	2.93 ± 0.05a	139	2.95 ± 0.07a	0.8240
	L3	148	3.43 ± 0.12b	116	4.2 ± 0.17a	0.0002
	Pupa	68	8.59 ± 0.17a	81	7.26 ± 0.18b	0.0000
	Preadult	68	24.13 ± 0.17a	81	22.22 ± 0.1b	0.0000
Female adult duration (d)	Adult	30	18.10 ± 1.82a	35	14.80 ± 1.72b	0.1821
Male adult duration (d)	Adult	38	21.00 ± 2.50a	46	15.96 ± 1.36b	0.0744
Female total longevity (d)	Whole life span	30	42.23 ± 1.82a	35	37.09 ± 1.72b	0.0343
Male total longevity (d)	Whole life span	38	45.13 ± 2.50a	46	38.13 ± 1.36b	0.0120
Mean longevity (d)	Whole life span	200	24.04 ± 1.16a	171	22.23 ± 1.03a	0.2477
APOP (d)	Female	24	4.29 ± 0.26a	29	4.34 ± 0.23a	0.8801
TPOP (d)	Female	24	28.08 ± 0.31a	29	26.55 ± 0.20b	0.0270
Fecundity (*F*; eggs per female)	Female	30	93.67 ± 15.09a	35	117.60 ± 23.59a	0.3903

Means in the same row followed by different letters are significantly different ($P < 0.05$) by using the paired bootstrap test.

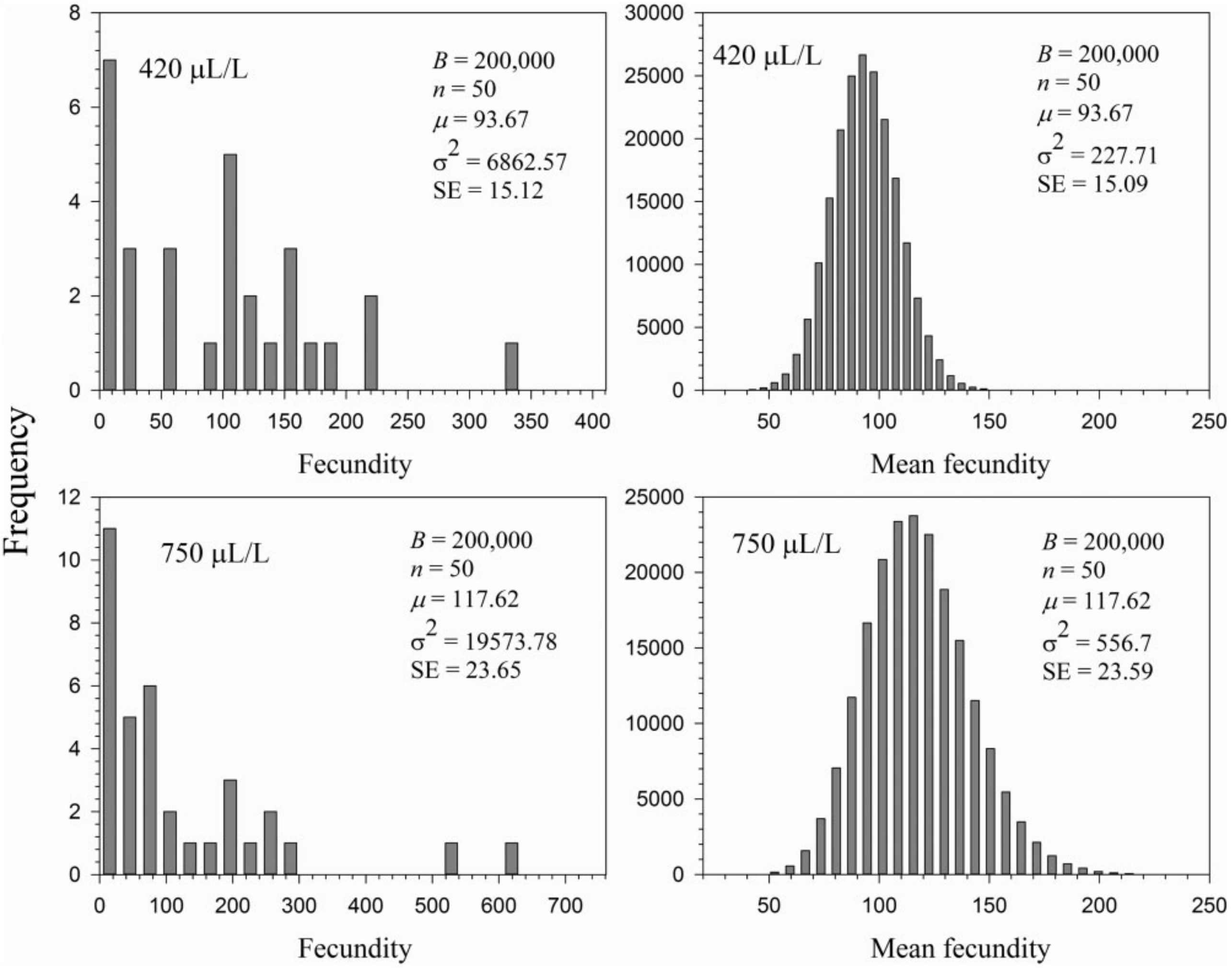

Fig. 1. Frequency distribution of fecundity and mean fecundity of *A. hygrophila* under different CO_2 conditions. The frequency distribution of mean fecundity was estimated by using 200,000 bootstraps.

while the bootstrap method with 100,000 replications, however, generates a normal distribution, which is important for further statistical analysis and comparison. In this study, the frequency distributions of mean fecundities ($B = 200{,}000$) of both treatment are normally distributed (Fig. 1); although the SEs estimated by using general statistics were similar to those estimated by using the bootstrap method, there were huge differences in variances.

Life Table and Population Parameters

The detailed age-stage-specific survival rates (s_{xj}) of *A. hygrophila* in the two different CO_2 conditions are plotted in Fig. 2. The parameter s_{xj} represents the probability that an egg of *A. hygrophila* will survive to age x and stage j. Overlapping among stages can be observed. In the 420 µl/liter CO_2 treatment, the probability that an individual surviving to the pupal stage is lower than that it is in the 750 µl/liter CO_2 treatment. However, those individuals developing to adult stages survived longer in 420 µl/liter CO_2 than in 750 µl/liter CO_2, which is also consistent with the longer total longevities (42.23 d for female and 45.13 d for male) in 420 µl/liter CO_2 shown in Table 1.

When the survival rates s_{xj} of different stages are pooled, the age-specific survival rate (l_x) produces a simplified overview of the survival history of the entire population (Fig. 3). Significant differences can be observed between the two different CO_2 conditions. In the 420 µl/liter CO_2 treatment, 34.5% of *A. hygrophila* survived longer than 20 d, while 42% survived longer than 20 d in 750 µl/liter CO_2. However, for those insects developing to the adult stage in 420 µl/liter CO_2, the survival rate curve of adult females and males extended to 73 and 90 d, respectively, while the survival rates of females and males in 750 µl/liter CO_2 ended at age 74 and 66 d, respectively (Fig. 2). In 420 µl/liter CO_2, the first reproduction occurred at age 26 d and reached its peak between ∼28–31 d; however, in 750 µl/liter $CO_{2,}$ reproduction began on age 24 d and reached peak fecundity at age 27 d. In 750 µl/liter CO_2, a few females produce more eggs during the age interval ∼45–66 d.

The population parameters of *A. hygrophila* are listed in Table 2. The intrinsic rate of increase ($r = 0.0798\ d^{-1}$), finite rate of increase ($\lambda = 1.0831\ d^{-1}$), and net reproductive rate ($R_0 = 14.05$ offspring) in 420 µl/liter were all lower than those in 750 µl/liter ($r = 0.0954\ d^{-1}$, $\lambda = 1.1000\ d^{-1}$, $R_0 = 20.58$ offspring). In 420 µl/liter, the mean generation time ($T = 33.10$ d), however, was longer than that in 750 µl/liter ($T = 31.71$ d).

The age-stage-specific life expectancy (e_{xj}) of *A. hygrophila* indicates the amount of time that an individual of age x and stage j is expected to live after age x (Fig. 4). The life expectancy of a new

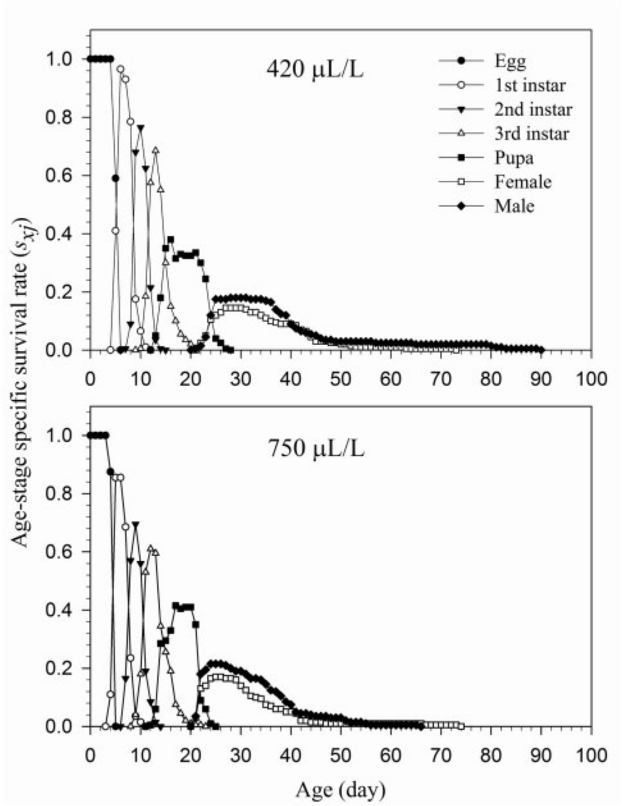

Fig. 2. Age-stage-specific survival rate (s_{xj}) of *A. hygrophila* reared in different CO_2 conditions.

born egg (e_{01}) is exactly the same as the mean longevity of all individuals in the cohort, e.g., the life expectancy of a new egg was 24.04 d in 420 μl/liter CO_2 and 22.23 d in 750 μl/liter CO_2 (Table 1). Due to the higher mortality found in the first instar and pupal stage, the life expectancy declined in the larval and pupal stage. When an individual survived to the adult stage, the life expectancy jumped to a high peak then declined gradually with aging. In general, our results showed that the life expectancy (e_{xj}) of *A. hygrophila* decreased with increasing concentration of CO_2 from 420 to 750 μl/liter.

The reproductive value is defined as the contribution of an individual at age x and stage j to the future population (Fisher 1930). The reproductive values (v_{xj}) of *A. hygrophila* are presented in Fig. 5. The reproductive value increased significantly when *A. hygrophila* began to produce viable eggs. In 420 μl/liter CO_2, the reproductive value jumped to 42.02 at age 22 d and reached a peak of 60.28 at age 27 d (Fig. 5). In 750 μl/liter CO_2, the reproductive value reached 46.11 at age 21 d and peaked at 71.80 at age 27 d, the v_{xj} value jumped again to 62.78 at age 42 d and remained at high values for an additional 20 d.

Population Projection

Huang and Chi (2013) pointed out that there are two types of information that can be obtained through life table study: the basic data (s_{xj}, f_{xj}, etc.) and the derived parameters (r, λ, T, etc.). Both intrinsic rate (r) and finite rate (λ) are the derived parameters and are calculated by assuming the population settles down to a stable age-stage distribution as time approaches infinity. As shown in Fig. 6, it is evident that neither of the *A. hygrophila* populations reached the "stable age" or "stable age-stage" distribution after 100 d when starting from an initial 10 eggs; therefore, it is inappropriate to predict the population size and stage structure using only the intrinsic rate or finite rate. The population projection based on the basic data (s_{xj} and f_{xj}) of a life table, however, offers a comprehensive understanding of the age and stage composition of a population during its growth.

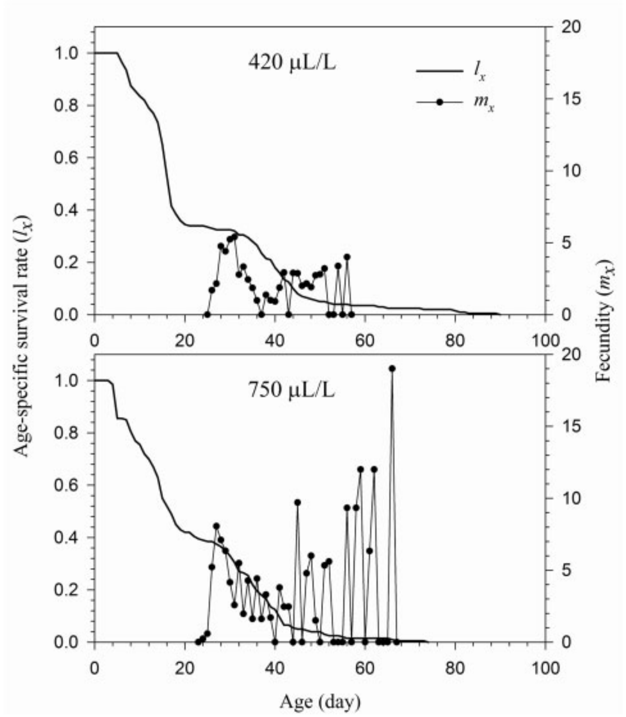

Fig. 3. Age-specific survival rate (l_x) and fecundity (m_x) of *A. hygrophila* reared in different CO_2 conditions.

The population projection showed that *A. hygrophila* reared in 750 μl/liter CO_2 concentrations would grow faster than in 420 μl/liter CO_2 (Fig. 6). Beginning with 10 eggs and reared under 750 μl/liter CO_2 conditions, the population would go through four generations, with the total population exceeding 41,000 after 100 d, while the flea beetle would go through four generations under 420 μl/liter CO_2 conditions, but would only attain a final population size of ~13,000 individuals.

Because of the rapid population increase potential of *A. hygrophila*, and the theoretical population size increasing to >1,300-fold of the initial 10 eggs within 100 d, we used equations 8 and 9 to describe the growth and dynamic of each life stage in logarithmic scale. The positive rate indicates an increase of a stage from time t to $t+1$, and the negative rate represents a decrease in stage size. Because the intrinsic rate (r) reflects the propagation potential of a population under ideal conditions when the population approaches stable age-stage distribution, the growth rate of all stages will approach the intrinsic rate ($r = 0.0798\,d^{-1}$ in 420 μl/liter and $0.0954\,d^{-1}$ in 750 μl/liter; Fig. 7).

Leaf consumption increased faster at the higher 750 μl/liter CO_2 concentration than it did at the 420 μl/liter CO_2 concentration. Total consumption increased from 36.07 mm^2 at 37 d to 500.78 mm^2 at 74 d under 420 μl/liter CO_2, but increased from 55.26 mm^2 at 37 d to 962.42 mm^2 at 70 d under 750 μl/liter—demonstrating that *A. hygrophila* would potentially be more effective against alligator weed by consuming a higher amount of the weed at 750 μl/liter CO_2, than at the lower concentration (Fig. 6).

Table 2. Population parameters (mean ± SE) of *A. hygrophila* under different CO_2 conditions

Parameter	420 µl/liter	750 µl/liter	P
Intrinsic rate of increase, r (d^{-1})	0.0798 ± 0.0072a*	0.0954 ± 0.0072a	0.1242
Finite rate of increase, λ (d^{-1})	1.0831 ± 0.0077a	1.1000 ± 0.0079a	0.2480
Net reproductive rate, R_0 (offspring)	14.05 ± 3.25a	20.58 ± 5.17a	0.5308
Mean generation time, T (d)	33.10 ± 0.84a	31.71 ± 0.82a	0.7430

*Means in the same row followed by different letters are significantly different ($P < 0.05$) using the paired bootstrap test.

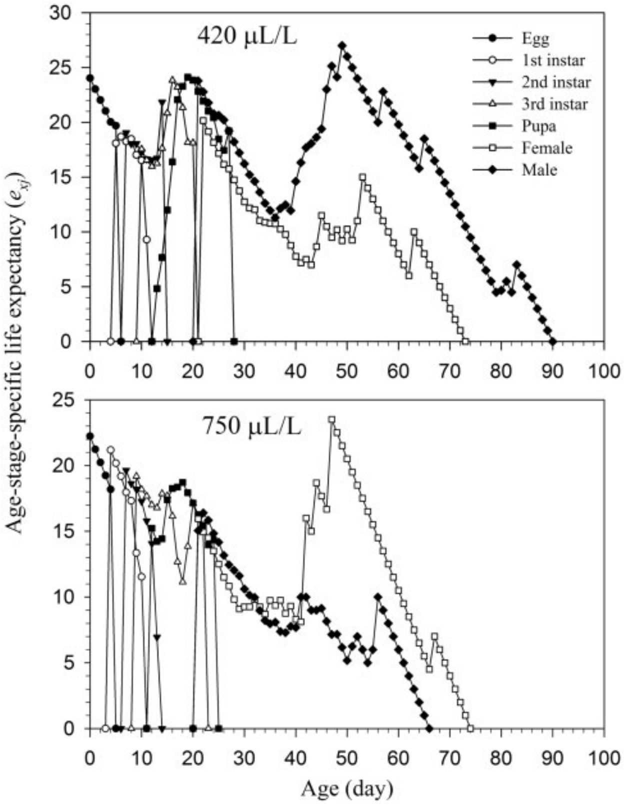

Fig. 4. Age-stage-specific life expectancy (e_{xj}) of *A. hygrophila* reared in different CO_2 conditions.

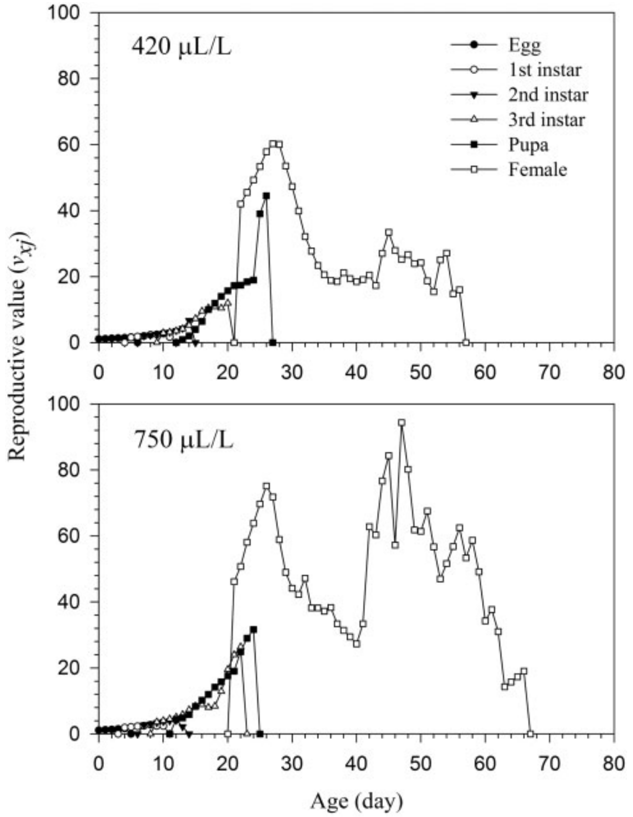

Fig. 5. Age-stage-specific reproductive value (v_{xj}) of *A. hygrophila* reared in different CO_2 conditions.

Discussion

Global warming has been a timely topic, and its effects on individual organisms and ecosystems have drawn international attention (Hughes 2000, Parmesan and Yohe 2003, Zvereva and Kozlov 2006). One of the major factors influencing global warming is the generation of greenhouse gases, especially CO_2. Because insects are ectothermic organisms, the effects of elevated temperature on their developmental rate are well documented and have been extensively studied (Yang and Chi 2006, Zhao et al. 2009, Hou and Weng 2010). Guo et al. (2012) reported that the population distribution and migration of flea beetles were affected by rising atmospheric temperature during the previous 20 years in China. Elevated CO_2 may profoundly interfere with the physiology and ecology of insects not only directly but may also act on them indirectly by affecting their host plants (Meng and Li 2005, Ge and Chen 2006, Guerenstein and Hilderbrand 2008). Although indirect effects of elevated CO_2 on insects merit further study, it is essential that the direct effects be documented to discover the effect of elevated CO_2 on insect occurrence and distribution, in order to predict possible shifts in insect population dynamics and community interactions in future environments (Guerenstein and Hilderbrand 2008).

Ge et al. (2010) showed that elevated CO_2 could prolong the larvae duration and delay the development of cotton bollworm larvae. Chen et al. (2006) reported that elevated CO_2 shortened the preoviposition period and the generation time, while accelerating the growth of the aphid, *Sitobion avenae* (F.) with increasing CO_2 concentration. Qian et al. (2015) and Li et al. (2013) reported that the egg stage and first-instar larval stage of *Frankliniella occidentalis* (Pergande), and the pupal duration of *Cnaphalocrocis medinalis* (Guenée) were significantly decreased in an elevated CO_2 concentration treatment. Similarly, the developmental times of the egg, first instar, and pupa of *A. hygrophila* were shortened in 750 µl/liter, while the developmental time of the third-instar larvae was increased in 750 µl/liter compared with those reared in 420 µl/liter. In summary, the total larval developmental duration was prolonged in 420 µl/liter CO_2. Akey and Kimball (1989) reported that the longevities of both sexes of adult beet armyworm, *Spodoptera exigua* (Hübner), were shortened in elevated CO_2. Fajer et al. (1989) reported similar phenomena in the buckeye butterfly, *Junonia*

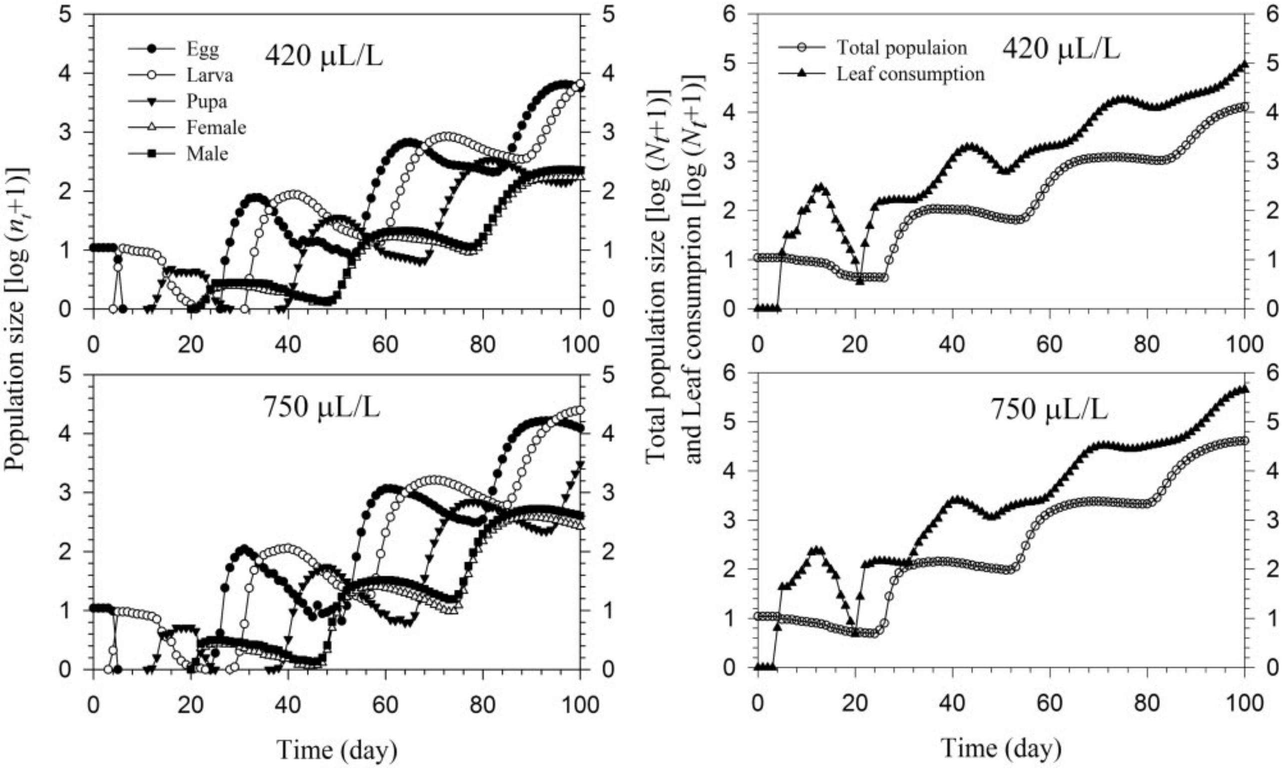

Fig. 6. Computer simulation of population growth and leaf consumption of *A. hygrophila* reared in different CO_2 conditions.

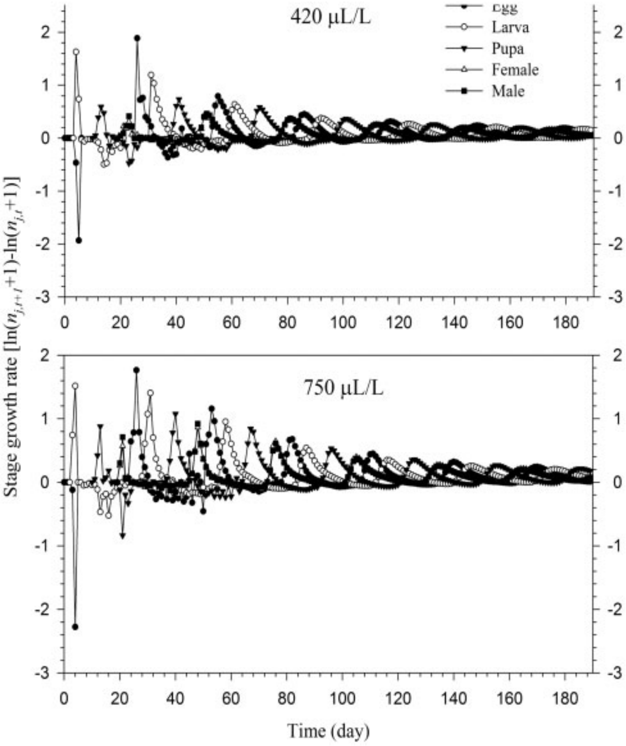

Fig. 7. Stage growth rate of *A. hygrophila* reared in different CO_2 condition.

coenia Hübner. When generation times are shortened, the number of annual generations will often increase, as reported for the aphid, *S. avenae*, when exposed to high CO_2 concentration (Chen et al. 2006). In the present study, we demonstrated that the TPOP is a more appropriate statistic from the point of view of demography, because it reflects the effect of the first reproduction from birth onward on the population parameters. The TPOP was 28.08 d in 420 µl/liter and 26.55 d in 750 µl/liter. As Lewontin (1965) demonstrated that earlier reproduction would result in a higher intrinsic rate, the faster population increase noted in *A. hygrophila* was observed in the intrinsic rate (Table 2) and computer simulation (Fig. 6).

The response of insects to atmospheric CO_2 concentration may also be reflected in an increase or decrease in fecundity. The fecundity of *S. avenae* was improved when reared in an elevated CO_2 environment (Chen et al. 2006). Our study demonstrated that the fecundity of *A. hygrophila* also increased under the elevated CO_2 concentration, which may be conducive to the proliferation of *A. hygrophila* population and its control effect on alligator weed *A. philoxeroides*. Moreover, the total preoviposition period in elevated CO_2 (750 µl/liter) was 1.53 d shorter than in the ambient CO_2 condition.

This study demonstrated the advantages of using the age-stage, two-sex life table theory in describing demography (Chi 1988, Yu et al. 2005). The stage differentiation can be observed in the s_{xj}, e_{xj}, and v_{xj} curves (Figs. 2, 4, and 5). The two peaks of v_{xj} showed that the population of *A. hygrophila* could increase faster at elevated CO_2 concentration than that at ambient CO_2 concentration, which is consistent with the fecundity shown in Table 1. As the traditional female age-specific cannot describe the stage differentiation and ignores the male population, the practical applications of traditional female age-specific life tables in population ecology and pest management are limited. The problems associated with of the traditional female age-specific life table are discussed in detail in Huang and Chi (2011).

Population projections based on life tables and stage-specific consumption rates can reveal the stage structure and damage potential of a pest population as shown in Tuan et al. (2014), Hou and Weng (2010), and Akca et al. (2015). Predicting the population size, stage structure, and leaf consumption capacity of *A. hygrophila* is important to the management strategy of the alligator weed *A. philoxeroides*. These parameters provide useful information for understanding the potential control efficacy of *A. hygrophila* against *A. philoxeroides*.

The daily leaf consumption of *A. hygrophila* larvae was similar at 420 μl/liter and 750 μl/liter, i.e., 23.45 and 23.77 mm^2/d, respectively, while the daily adult consumption under 750 μl/liter (37.83 mm^2/d) was significantly lower than that under 420 μl/liter (49.95 mm^2/d). Population projection incorporated with leaf consumption showed, however, that the consumption of the population under 750 μl/liter was higher than that of 420 μl/liter due to the higher growth rate. Our results demonstrated that the control efficacy of natural enemies against a pest species should not be evaluated based solely on individual consumption. It is essential that the growth rate of natural enemies should be taken into consideration as well. This, once again, demonstrates the advantage of using the two-sex life table in life table analysis and its application in biological control programs.

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