

## Life tables and demographic statistics of Russian wheat aphid (Hemiptera: Aphididae) reared at different temperatures and on different host plant growth stages

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**Key words.** Hemiptera, Aphididae, *Diuraphis noxia*, Russian wheat aphid, life table, insect demography, intrinsic rate of increase, population ecology

**Abstract.** Laboratory experiments were used to investigate the influences of 25 combinations of temperature and barley plant growth stage ( $5 \times 5$  factorial combination of temperature and barley plant growth stage) on the development, survival and reproduction of the Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko). For each of the 25 treatments, the developmental time and nymphal production of 72 RWA individuals were recorded (1800 RWA in total) throughout their entire lifetimes. The collected data were used for analyzing demography, modelling phenology, and simulating population growth of RWA. In this paper, the results of demographic analyses are reported. Specifically, for each treatment, cohort life tables, reproductive heterogeneity tables (parity and birth intervals), and reproductive schedule tables were constructed, and demographic parameters such as intrinsic rate of increase, life-span, fecundity, life table entropy, etc. calculated. Based on these analyses, the most important summary demographic statistics are reported. Using the intrinsic rate of increase ( $r_m$ ) as an example, a procedure is demonstrated that builds a dynamic  $r_m$  model by applying the Best Subset Regression approach. A more comprehensive (considering reproductive heterogeneity and schedule tables) yet concise (comprising dynamic  $r_m$  models) demographic model than that based on standard life table analysis alone is presented.

### INTRODUCTION

Russian wheat aphid (RWA), *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), was first detected in Texas in 1986, and by the early 1990's it had become established in the US west of the 100th meridian and in three adjoining western Canadian provinces (Webster et al., 1996). In its first decade in North America, the RWA caused significant damage and posed a serious threat to wheat and barley production in the United States and Canada. Although the damage caused by RWA now seems to be under control, it is still important to understand this aphid's population demography. For example, Qureshi & Michaud (2005) compare the biology of RWA with that of the two other cereal aphids, the greenbug [*Schizaphis graminum* (Rondani)] and bird cherry-oat aphid [*Rhopalosiphum padi* (Linnaeus)]. They discuss the importance of the differences and especially the interference among the three aphid species in the development and evaluation of new resistant wheat cultivars.

Insect demography and phenology have always been very important research fields in entomology and pest management, and Carey (2001) and Ikemoto (2005) present state-of-the-art reviews of the two fields. Demography and phenology are frequently the focus of studies on aphid ecology and biology (Hentz & Nuessly, 2004; Liu, 2004; McCornack et al., 2004; Qureshi & Michaud, 2005).

Prior to this study, several laboratory studies have examined the effects of temperature on RWA development, survival and reproduction (Michels & Behle, 1988, 1989; Kieckhefer & Elliott, 1989; Behle & Michels,

1990; Girma et al., 1990). Field research on RWA has mainly focused on its over-wintering period (Harvey & Martin, 1988; Aalbersberg et al., 1989; Butts, 1992; Armstrong & Peairs, 1996). While understanding over-wintering is important, overall RWA population dynamics cannot be understood or predicted without a thorough knowledge of the population changes during the rest of the annual cycle. In general, they are smoother as the environmental conditions then are less severe than in winter. Development, survival and reproduction data obtained from laboratory experiments under controlled environmental conditions are quite useful for modelling non-overwintering stage population dynamics, but such quantitative models of RWA population development have yet to be developed. In addition, RWA development and demography studies almost exclusively used wheat plants rather than barley (Michels & Behle, 1988; Kieckhefer & Elliott, 1989; Girma et al., 1990).

Laboratory experiments were used to collect the required data to develop RWA population phenology and growth models. The effect of 25 different temperature and barley plant growth stage regimes on RWA development, survival and reproduction was determined. In this paper, we report the population demographic statistics needed for producing traditional cohort life tables and analyze the effect of temperature and barley plant-growth stage on RWA population growth.

### MATERIAL AND METHODS

The experiment was conducted in two growth chambers. Treatments were factorial combinations of 5 temperatures and 5 barley plant growth stages. Temperature regimes were 8–1°C,

17–10°C, 23–16°C, 28–21°C, 33–26°C, fluctuating on a 14L : 10D rectangular-wave cycle (where the higher constant temperature coincided with the light phase and the lower temperature coincided with the dark phase). Hence, mean temperatures weighted by photoperiod were 5.1, 14.1, 20.1, 25.1 and 30.1°C, respectively. Barley plant growth stages were two-leaf, tillering, flag leaf, inflorescence, and soft dough, which correspond to Zadoks scale (Zadoks et al., 1974) 12, 23, 39, 59, and 85, respectively. Spring barley, variety “Excel”, was sown in 6-cm diameter pots in a greenhouse. Every two days, new barley plants were sown to continue the supply of barley plant leaves of different growth stages.

Russian wheat aphids used in the experiment were from a laboratory colony maintained in a growth chamber, which was originally collected from fields near Moscow, Idaho, USA. Each aphid was reared in a Petri dish containing a clipped spring barley leaf placed on wet filter paper and secured at the leaf ends with small pieces of filter paper. As indicated previously, leaves from barley plants at five different growth stages were used in different treatments, respectively. Behle & Michels (1990) compared four different plant media (whole plants grown in peat moss/perlite soil, whole plants grown hydroponically in Hoagland’s solution, exercised leaves inserted in a benzimidazole-doped agar media, and excised leaves inserted in water-saturated paper towels) to determine if different plant media affected RWA life table statistics. They concluded that differences in RWA development and reproduction on plants grown in the different media were very small. In a preparatory experiment, we found that maintaining appropriate humidity inside the Petri dish was critical, especially at high temperatures; hence, a 12 × 12 cm<sup>2</sup> piece of parafilm® paper was inserted between the dish and cover to prevent desiccation.

Experiments began with the preparation of newly-born first-instar nymphs. About 6 p.m., about 200 female adults from the colony were transferred to 72 Petri dishes prepared as previously described. These females were left to reproduce at room temperature until approximately 11 p.m. Then the dishes were examined and RWA nymphs transferred gently with a fine brush to establish one nymph per dish. This procedure was finished at midnight and Day one of the experiment began with the 72 Petri dishes moved into the growth chamber. These procedures controlled age differences among individuals within a cohort (treatment) to 6 h. Survival, molting and nymphal production of each aphid were recorded daily until death. New progeny were removed daily; every two days, leaves were replaced from plants that had just reached the required growth stage. The entire experiment required 9 months. Given the extensive data collected from the experiments (1800 RWA in 25 treatments), this paper exclusively focuses on the survival and reproduction statistics of RWA demography, and the development and phenology aspects of RWA is reported elsewhere (Ma & Bechinski, 2008). In addition to using standard statistical software BMDP Version 7.0 (BMDP Inc., 1993) for Best Subset Regression Analysis, we developed a computer program for constructing cohort life tables and calculating demographic statistics, the codes for which were included in Ma (1997) as Appendix I of Chapter 2.

## RESULTS

### Cohort life tables, reproductive statistics, and summarized demographic statistics

All terminology and formulae for computing demographic statistics follow Carey (1993) and the computations were performed using a computer program documented in Ma (1997) (Appendix I of Chapter 2).

This program tabulated and printed out the life tables, reproductive heterogeneity and schedule tables as defined in Carey (1993). Because listing complete life tables and tables of reproduction for all 25 treatments would require too much space, these tables are not presented in this paper. However, full tables for one treatment (20°C and two-leaf barley growth stage) are published in Ma (1997), and complete results for all 25 treatments can be computed and printed out by running the above-mentioned computer program. Here, a summary of the most important demographic statistics is presented in Table 1, based on the results for the 25 treatments documented in Ma (1997). In addition, it should be noted that in this paper we only report the reproductive statistics of RWA, as the developmental aspects are published in Ma & Bechinski (2008).

The variation in reproduction among individuals vs. that of the “average” female within a cohort is rarely analyzed in insect population studies, although it has been advocated for quite long time (e.g., Carey, 1993). Reproductive parity and birth intervals are two important parameters that measure heterogeneity in reproduction among individuals in a population. Daily parity describes the heterogeneity (or consistency) of nymphal production in a cohort at a specific age (Carey, 1993). The daily parity table lists the percentage of RWA females at a specific age that produce a particular number of nymphs. Birth interval indicates the daily reproduction of the aphids. While reproduction parity measures the number of nymphs produced per day, the birth interval indicates the average number of days between two reproductive events for an average individual (Carey, 1993). The reproductive parity and birth interval tables for RWA are computed and documented in Ma (1997), but omitted here to save space. Instead, here we only report the most important summary statistics in Table 1.

The per-capita age-specific fecundity rates over specified age intervals form a reproductive age schedule (Carey, 1993). A gross schedule does not consider mortality where a net schedule weights reproduction by the proportion of the cohort that survives to each age class. The reproductive age schedule includes the reproductive rates of the different age classes. The calculations are based on an average individual and do not consider reproductive heterogeneity among individuals. The reproductive age schedule and heterogeneity measures such as parity and birth interval together describe the characteristics of insect populations more completely. As previously the reproductive age schedule tables are omitted and only the crucial summary statistics are presented in Table 1.

In summary, the experiment data were used to construct: age-specific cohort life tables, reproductive parity and birth interval tables, and reproductive age schedule tables. The tables for one treatment are fully documented in Ma (1997), and complete results for all 25 treatments can be calculated and printed using the computer program in Appendix I of Chapter 2 of Ma (1997). Due to limitations on space, only a summary of the most

TABLE 1. Population demographic statistics of RWA reared at different temperatures and on different barley plant growth stages.

No.	Temp.	Stage	AgeC	Entro	APRP	AALS	AMDL	ARDL	BIAA	BIAM	LIFE-span	NFD	MAGF	MANF	NF	$r_m$
1	5.08	12	108	0.631	6.97	40.1	33.14	9.28	4.32	3.57	48.903	0.11	81.48	72.86	4.000	0.019
2	5.08	23	103	0.883	5.29	36	30.71	10.36	3.48	2.97	31.069	0.07	75.72	69.55	2.208	0.012
3	5.08	39	96	0.534	4.97	34.8	29.83	11.63	2.99	2.57	49.000	0.21	70.80	63.32	6.306	0.030
4	5.08	59	101	0.639	5.93	40.33	34.4	12.83	3.14	2.68	46.583	0.18	78.04	67.63	6.056	0.028
5	5.08	85	91	0.670	6.68	34.07	27.39	10.5	3.24	2.61	40.236	0.13	68.28	63.49	4.361	0.024
6	14.08	12	57	0.378	1.22	25.95	24.73	21.3	1.22	1.16	33.431	1.85	28.51	27.00	45.431	0.173
7	14.08	23	63	0.551	1.31	28.88	27.56	22.46	1.29	1.23	29.847	1.17	31.26	27.63	32.917	0.150
8	14.08	39	68	0.400	1.33	29.21	27.88	21.88	1.33	1.27	35.611	1.27	33.62	27.63	35.736	0.157
9	14.08	59	61	0.489	1.66	27.28	25.62	17.42	1.57	1.47	31.056	0.89	33.24	27.13	22.708	0.142
10	14.08	85	67	0.480	1.88	29.36	27.48	19.1	1.54	1.44	33.361	0.85	38.42	32.08	22.653	0.114
11	20.08	12	40	0.376	0.76	16.85	16.08	14.49	1.16	1.11	22.069	2.67	20.04	16.74	43.000	0.278
12	20.08	23	38	0.675	0.56	14.78	14.22	12.19	1.21	1.17	15.139	1.22	22.75	18.82	16.931	0.169
13	20.08	39	33	0.696	0.7	13.27	12.57	11.5	1.15	1.09	13.250	1.04	22.69	18.51	12.181	0.148
14	20.08	59	29	0.659	0.76	9.62	8.86	7.48	1.29	1.18	11.792	0.68	19.49	16.73	6.125	0.113
15	20.08	85	26	0.649	0.89	8.11	7.21	5.86	1.38	1.23	10.750	0.59	18.55	15.89	4.492	0.095
16	25.08	12	31	0.461	0.89	13.46	12.57	11.46	1.17	1.1	17.125	2.64	16.06	14.32	33.194	0.288
17	25.08	23	31	0.602	0.81	10.33	9.51	8.63	1.2	1.1	12.569	1.76	17.45	13.71	15.903	0.226
18	25.08	39	29	0.897	1.13	11.93	10.8	10.33	1.15	1.05	7.903	0.66	18.88	15.94	5.319	0.112
19	25.08	59	26	0.927	0.86	9.43	8.57	5.86	1.61	1.46	5.222	0.11	17.00	14.55	0.931	-0.005
20	25.08	85	26	1.058	1.4	8.8	7.4	5.4	1.63	1.37	4.556	0.09	20.51	17.36	0.694	-0.020
21	30.08	12	16	0.723	–	–	–	–	–	–	5.292	–	–	–	–	–
22	30.08	23	13	0.698	–	–	–	–	–	–	3.681	–	–	–	–	–
23	30.08	39	13	0.764	–	–	–	–	–	–	3.764	–	–	–	–	–
24	30.08	59	8	0.577	–	–	–	–	–	–	2.917	–	–	–	–	–
25	30.08	85	5	0.454	–	–	–	–	–	–	2.292	–	–	–	–	–

Abbreviations: No. – treatment number (1–25); Temp. – temperature (°C); Stage – growth stage of spring barley; AgeC – the number of age classes in a treatment; Entro. – entropy of life table; APRP – average pre-reproduction period; AALS – average adult life span; AMDL – average mature days lived; ARDL – average reproductive days lived; BIAA – birth interval against adulthood; BIAM – birth interval against mature adult; LIFE – average LIFEspan of an aphid individual; NFD – nymphs per female per day; MAGF – mean age gross fecundity; MANF – mean age net fecundity; NF – net fecundity (net reproductive rate);  $r_m$  – intrinsic rate of increase.

important reproductive statistics from those tables is presented in Table 1.

As indicated previously, the definitions and formulae for the demographic statistics in Table 1 can be found in Carey (1993). Although the use of these demographic statistics has been advocated in insect demography for quite a long time (e.g., Carey, 1993), most published studies on insects often only present cohort life tables and their summary statistics. The reproductive heterogeneity and reproductive schedule tables, as well as their summary statistics, are often not analyzed in the literature of insect demography. To the best of our knowledge, there is no information on the reproductive heterogeneity (parity and birth intervals) and reproductive schedule tables of RWA in the literature. As elaborated in Carey (1993, 2001), these demographic statistics are of significant theoretical and practical value for insect demography. This motivated the relative detailed analysis of RWA demographic data in Ma (1997) and this report of the summary statistics.

We suggest that the reason why reproductive heterogeneity and schedule tables have not been as widely adopted

as cohort life tables might be related to the origin of these analysis techniques. Historically, insect demography borrowed many major concepts and methodologies from human demography and public health research (e.g., Carey, 1993, 2001). The importance of reproductive heterogeneity and schedule tables in human population studies is necessary for more accurate study of human population growth. For example, they may help to reveal the mechanisms resulting in growth or decline in a population caused by individual or group variation. We believe such kind of analysis should also be very important in the study of insect population growth.

We also conjecture that the phenomenon in insect demography, discussed above, might be related to a reality that these statistics alone, if not correlated with environment factors, might be inconvenient for application. For example, in our case and perhaps in insect demography at large, there is no standard way of synthesizing the statistics from various treatments. For this reason, the relationship between the demographic statistics

and environmental factors, which in our case are temperature and plant growth stage, are explored below.

### Intrinsic rate of increase ( $r_m$ ) at different temperatures and barley plant growth stages

The objective of this subsection is to explore the quantitative relationship between demographic statistics and environmental factors. In other words, the goal is to synthesize the demographic statistics recorded under various environmental conditions (as reported in Table 1) into more compact mathematical models. The population intrinsic rate of increase ( $r_m$ ) is chosen as a demonstrative example, but other summary statistics in Table 1 could be modelled similarly. Another reason for selecting  $r_m$  is its well-recognized importance in population demography.

The relationship between the intrinsic rate of increase ( $r_m$ ) and temperature and plant growth stage was modelled using the Best Subsets Regression technique implemented in the BMDP 9R program (BMDP, 1993). Best Subset Regression is similar to stepwise regression. However, unlike stepwise regression, in which the final selected equation depends heavily on F-values, the Best Subsets Regression identifies the “best” subsets of variables that will be the independent variables of the “best” regression model, according to some criterion. Five criteria used to identify “best” subsets are the sample  $R^2$ , adjusted  $R^2$ , Mallows’  $C_p$  statistic, residual mean square and  $F$ -value. Best subsets are those that satisfy the specified selection criterion better than other subsets (BMDP, 1993).

As indicated previously, of the demographic parameters listed in Table 1, the intrinsic rate of increase ( $r_m$ ) was chosen to illustrate the effects of various temperatures and plant growth stages on Russian wheat aphid demography. The Best Subset Regression is used to model the relationship between  $r_m$  and temperature and plant growth stage because it provides an effective way of obtaining the best fit with possibly the least number of variables. The sets of variables used to generate the best subset regression equation for RWA  $r_m$  were

square surface:  $t, s, t^2, s^2, ts$

cubic surface:  $t, s, ts, t^2s, s^2t, t^3, s^3$

linear combinations of exponential, power functions of  $t$  and  $s$ .

Here  $t$  is temperature and  $s$  barley growth stage. The selected Best Subset Regression equation is

$$r_m = [-0.1168 + 1.7581(\frac{t}{30}) - 1.1452(\frac{t}{30})^2 + 0.2006(\frac{s}{9})^2 - 0.7014(\frac{t}{30})(\frac{s}{9})]^2 \quad (1)$$

Residual Mean Square = 0.000903

Mallow’s  $C_p$  = 4.05

Adjusted Square of Multiple Correlation Coefficients ( $R^2$ ) = 0.9432

Multiple Correlation Coefficient = 0.9781

$F$ -value of Regression = 71.59

$p$ -value = 0.0000

The very low  $p$ -values for overall regression and regression coefficients, small standard errors for model parameters and the values of the statistics used to select the best subset regression all indicate that the model is

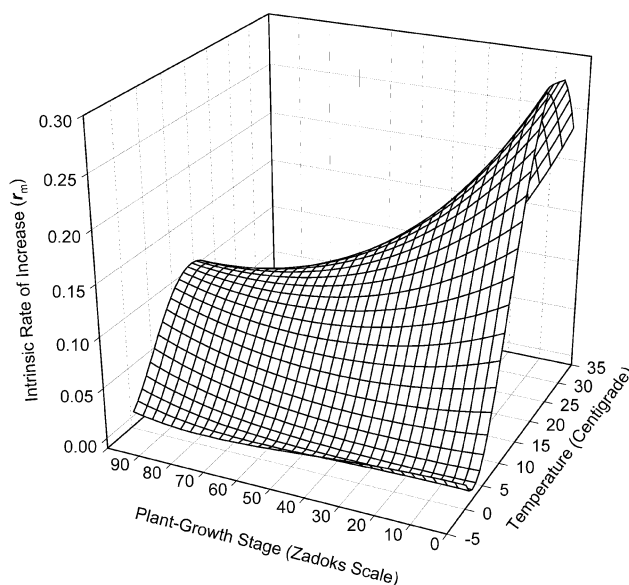


Fig. 1 Relationship between RWA intrinsic rate of increase ( $r_m$ ), temperature and barley plant-growth stage. This relationship is described by Equation (1).

reliable. A three-dimensional graph of the best subset regression (Equation 1) is depicted in Fig. 1.

The graph shows that high temperatures and older plant growth stages are unfavourable for RWA population growth and intermediate temperatures (14°C–25°C) and younger plant growth stages are more favourable. Other parameters listed in Table 1 also support this general conclusion. The RWA also survived longer at lower temperatures but produced fewer progenies. At high temperatures (e.g., 30°C) the life-span of RWA is extremely short and they do not reproduce. The results reported here present a comprehensive yet concise description of RWA demographic characteristics and their responses to environmental factors such as temperature and host plant growth stage.

### DISCUSSION

In this subsection, we first try to summarize the existing demographic studies on RWA and then put our study into perspective.

Aalbersberg & du Toit (1987) report that RWA reproduction rates (total nymphs produced by a female) ranged from 72 to 81.5 nymphs at fluctuating temperatures that averaged from 13 to 17.3°C. In contrast, Webster & Starks (1987) report average production of 30–50 nymphs per female under three fluctuating temperature regimes that averaged from 13.2 to 17.2°C, while Kieckhefer & Elliott (1989) report from 15.0 to 46.9 nymphs per female for apterae and 13.0 to 31.8 for alatae. Direct comparison of the results from these studies is difficult because factors other than temperature, such as host plant growth stage and photoperiod, which strongly influence reproduction, also differed in these studies. A more subtle, but not unimportant reason is that some authors “average” total nymphs across all individuals in the sample

(including those that died before reproduction), while others average the results only for those that reproduce.

Aalbersberg et al. (1989) report that RWA populations in fields of wheat increased exponentially between the period of stem elongation [Zadoks Growth Stage (Z.G.S.) = 30] and completion of ear emergence (Z.G.S. = 59), and densities declined dramatically during the period of plant senescence. Girma et al. (1990) report that RWA intrinsic rate of increase ( $r_m$ ) was highest at 18–21°C for all wheat growth stages, except tillering plants stage on which the maximum  $r_m$  was achieved at 27–29°C. The prediction of our  $r_m$ -model (Fig. 1) is consistent with their field observations.

The Russian wheat aphid is quite cold-tolerant (Harvey & Martin, 1988). When exposed to 0°C for 5 days in the laboratory, 96% survived; after 40 days exposure, 3% survived. Survivorship after 1-h or 5-days exposure to –10°C was 66% or 24%, respectively; 6% survived 16 h exposure to –20°C. Mean supercooling points ranged from –26.8°C for the first instar to –24.9°C for adults. Although the supercooling point and the ability to survive cold temperatures in the field are not necessarily closely related (because mortality in the field can occur at temperatures well above the supercooling point), the comparatively low supercooling point does indicate the great cold hardiness of this aphid. Under our experimental conditions, 50% survived for one month and 10% survived beyond 100 days, when kept at 1–8°C temperature regime (mean = 5°C) (Ma, 1997).

Michels & Behle (1989) investigated the effects of constant (10°C) and fluctuating (5–15°C and 1–19°C, average = 10°C) temperature regimes on development, reproduction and intrinsic rate of increase of the Russian wheat aphid, green bug (*Schizaphis graminum*) and bird cherry-oat aphid (*Rhopalosiphum padi*). Significant differences in nymphal development and total lifespan were observed both among species within a temperature and among temperature treatments for a species. The intrinsic rate of increase of all three species was highest when kept in a fluctuating temperature regime of 1–19°C. Whether fluctuating temperature enhances population growth is a controversial issue (Siddiqui & Bralow, 1973). Michels & Behle (1988) earlier reported the survival and reproduction of RWA kept at six constant temperatures (5, 10, 15, 20, 25, or 30°C). They found that RWA total life span decreased significantly with increase in temperature. They attribute the decrease in lifespan to a decrease in time required for nymphal development with increase in temperature. Adult life span increased between 5 and 15°C but decreased significantly between all other temperatures. The authors conclude that fecundity was not a linear function of adult age but depended on temperature and age. The average number of nymphs produced per aphid per day increased at each temperature regime from 5 to 20°C, but decreased significantly beyond 20°C. The trend in natality as a function of temperature was symmetrical (approximating a normal curve), with no significant differences between 5 and 30°C, 10 and 25°C, and 15 and 20°C. Similar observations on the effect of tem-

perature on aphid natality are reported by Nowierski et al. (1983) and Ballou et al. (1986).

To put this study into perspective relative to existing research on RWA demography, we stress the following: (1) This paper does not include detailed demographic tables and only reports summary statistics. Although it is difficult to compare the results with those of existing studies due to these omissions, the detailed report of this study in Ma (1997) is consistent with existing studies. (2) We focus on the most important demographic summary statistics (Table 1). In particular, Table 1 contains summary statistics on reproductive heterogeneity and schedule tables. These statistics, despite being actively advocated in the literature (e.g., Carey 1993, 2001), have not been used in insect demography as widely as those based on the well-known cohort life tables. To the best of our knowledge, the reproductive heterogeneity and schedule statistics for RWA have not been reported previously. We believe these statistics are as important for modelling RWA population growth, as they have been in human demography, where these statistics are often carefully analyzed. (3) Even with the summary statistics presented in Table 1, it is still necessary to further synthesize the information so that the demographic statistics for the different environmental conditions can be condensed into dynamic models. This procedure is demonstrated by utilizing Best Subset Regression to model population intrinsic rate of increase ( $r_m$ ) for a range of different environmental conditions. This procedure can be similarly applied to modelling the other demographic statistics in Table 1. It is our opinion that these demographic statistics (summarized in Table 1) and dynamic models developed for these statistics [such as that for  $r_m$  modelled by Equation (1) and presented as a graph in Fig. 1] using Best Subset Regression offer more comprehensive but still concise information for modelling insect population growth.

**ACKNOWLEDGEMENTS.** Ma wishes to thank J. Johnson, M. Klowden, J. McCarffrey, B. Shafii, M. Stock, University of Idaho, and Sharron Quisenberry, Iowa State University, for their valuable advices and help during his doctoral study when this research was conducted. Special thanks to V. Nebling for his assistance in laboratory experiment.

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Received July 29, 2008; revised and accepted November 4, 2008