Demographic Traits of *Tetranychus urticae* (Acari: Tetranychidae) on Leaf Discs and Whole Leaves

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ABSTRACT   Life tables of twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), were studied on leaf discs and whole leaves of the common bean plant, *Phaseolus vulgaris* L. Data were analyzed based on the age-stage, two-sex life table theory. Durations of deutonymph stage, total preadult stage, and preoviposition period of mites reared on whole leaves (1.22, 7.6, and 0.29 d, respectively) were significantly shorter than those reared on leaf discs (1.73, 8.2, and 0.89 d, respectively). The lifetime fecundities were 22.81 and 12.05 offspring on whole leaves and leaf discs, respectively. Although hooked trichomes on the lower surface of the bean leaf contribute to adult mortality, spider mites successfully survive and reproduce on bean plants. The intrinsic rate of increase on whole leaves ($0.235\,\mathrm{d}^{-1}$) was higher than that on leaf discs ($0.159\,\mathrm{d}^{-1}$). Higher intrinsic rate and fecundity found in mites reared on whole leaves may be due to the higher nutritional quality of whole leaves over leaf discs. We suggest that whole leaves should be used in future studies to better simulate realistic life history characteristics. The advantages of using age-stage, two-sex life tables over female age-specific life tables are discussed.

چکیده: جدول های زندگی کنه تارتن دو لکه ای Koch *Tetranychus urticae* روی دیسک های برگی و نیز برگ های کامل گیاه لوبیا *Phaseolus vulgaris* L. مطالعه شدند. داده ها بر اساس تئوری جدول زندگی سنی– مرحله رشدی دوجنسی تجزیه و تحلیل شدند. دوره رشدی مرحله دئوتونمف، کل دوره قبل از بلوغ و دوره قبل از تخمریزی روی برگ های کامل (به ترتیب ۱/۲۲، ۷/۶ و ۰/۲۹ روز) به طور معنی داری کوتاه تر از دوره های بدست آمده روی دیسک های برگی (به ترتیب ۱/۷۳، ۸/۲ و ۰/۸۹ روز) بودند. باروری کل دوره زندگی روی برگ های کامل ۲۲/۸۱ و روی دیسک های برگی ۱۲/۰۵ بود. اگرچه موهای قلاب مانند موجود در سطح زیرین برگ های لوبیا باعث مرگ و میر برخی کنه های کامل می شوند ولی کنه ها می توانند با موفقیت روی گیاه لوبیا زندگی کرده تولید مثل کنند. نرخ ذاتی افزایش جمعیت روی برگ های کامل (۰/۲۳۵ روز ‎⁻¹) بیشتر از نرخ روی دیسک های برگی (۰/۱۵۹ روز ‎⁻¹) بود. نرخ بالای افزایش ذاتی و باروری بالا روی برگ های کامل ممکن است در اثر کیفیت غذایی بهتر برگ های کامل باشد. ما اعتقاد داریم بهتر است از برگ های کامل استفاده گردد تا بتوان ویژگی های تاریخچه زیستی واقعگراتری را نشان داد. مزایای جدول زندگی سنی– مرحله رشدی، دوجنسی بر جدول زندگی رایج بر اساس جنس ماده و ویژه سنی مورد بحث می باشند.

The twospotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), is a serious cosmopolitan pest species commonly found on many horticultural and agricultural crops. More than 900 species of host plants have been recorded for *T. urticae* (Bolland et al. 1998). It has been recognized as an exotic species for Taiwan and is now considered to be the second most important spider mite among the 10 major species present in Taiwan (Ho 2000).

Life tables are an important tool in the study of population ecology and invasiveness of introduced species (Sakai et al. 2001), conservation (Wilcox and Murphy 1985), demographic ecotoxicology (Stark and

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Banks 2003), harvesting theory (Chi 1994), and pest control timing (Chi 1990). Life tables of *T. urticae* mites maintained on leaf discs have been studied using traditional female age-specific life table methods by a number of researchers (Shih et al. 1976; Wermelinger et al. 1991; Krips et al. 1998; Bounfour and Tanigoshi 2001; Kasap 2002, 2004; Marcic 2003; Sim et al. 2003; Martínez-Villar et al. 2005). Problems encountered when using the female-based age-specific life table have been discussed by Chi (1988) and Chi and Yang (2003). An age-stage, two-sex life table theory was developed to resolve these problems by including the stage differentiation and male population (Chi and Liu 1985, Chi 1988). The age-stage, two-sex life table theory has been used for beneficial as well as for pest insects (Yu et al. 2005, Amir-Maafi and Chi 2006, Chi and Su 2006, Mo and Liu 2006). In this study, we determined the life table of *T. urticae* based on the age-stage, two-sex life table theory. Many of the studies on *T. urticae* have been conducted using leaf discs. Because decay and desiccation of leaf discs affect the leaf quality, mites need to be transferred to new discs every 3–4 d (Haque et al. 2007). Other problems have been reported when leaf discs have been used, including mite runoff and mites becoming trapped in the barriers (Kabir et al. 1993, Bounfour and Tanigoshi 2001, Auger et al. 2003, Kavousi and Talebi 2003). Biochemical and physiological differences between plant tissues of leaf discs, excised whole leaves and intact leaves attached to plants have been noticed in beetles (Huang et al. 2003). In addition, evidence linking the effects of nutritional quality of the host plants to life history traits and population parameters of *T. urticae* have been demonstrated by Wermelinger et al. (1991). Based on these observations the ideal situation would be to use whole plants. However, due to the difficulties involved and complexities encountered when whole plants were used in life table studies we, instead decided to use whole leaves as well as leaf discs (the traditional method) to determine whether there were measurable adverse effects attributable to using the leaf discs.

Materials and Methods

Plants. Seeds of the common bean plant, *Phaseolus vulgaris* L., were sown in plastic pots (10.5 cm in diameter, 8.5 cm in height) filled with the substrate Potgrond H (Klasmann-Deilmann GmbH, Geeste, Germany). Pots were kept in large trays for ease of transportation. Plants were maintained at $25 \pm 1°C$, $65 \pm 5\%$ RH, and a photoperiod of 16:8 (L:D) h. When the plants reached 30 cm height, they were used for rearing mites.

Spider Mites. Spider mites were obtained from a laboratory colony reared on *P. vulgaris* in the Taiwan Agricultural Research Institute, Taichung, Taiwan, Republic of China. Mites were mass reared on plants kept at the above conditions.

Life Table Study on Leaf Discs. Twenty-millimeter-diameter discs of trifoliate leaves of *P. vulgaris* were placed upside down on water-saturated cotton

wool pads in 9-cm petri dishes, and a single female was placed on each leaf disc. One hundred petri dishes were then placed in growth chambers ($25 \pm 2°C$, $80 \pm 5\%$ RH, and a photoperiod of 16:8 [L:D] h). After 1 d, a single egg was left on each leaf disc, and the remaining eggs and female were removed. The development and survival were recorded every 24 h until the death of each individual. For females, the daily fecundity of individual mites was also recorded. When an individual developed to the adult stage, it was paired with an individual of the opposite sex from the cohort. Because more females than males emerged, additional young males from the mass rearing colony were used for mating when necessary. Data from these males were not included in life table analyses. Missing individuals were excluded from the analyses. Leaf discs were normally replaced weekly, unless obvious wilt, desiccation, or other abnormalities were noticed, requiring earlier replacement.

Life Table Study on Whole Leaves. Fifty trifoliate leaves with petioles were removed from the plants. The petioles were wrapped with cotton wool and inserted into individual glass tubes (1 cm in diameter by 3 cm in height) filled with water. One female adult mite was placed on each leaf. Each leaf was then placed into separate transparent plastic cups (9 cm in diameter by 5.5 cm in height) and capped. A 1-cm^2 hole was cut in the caps for ventilation. The cups were then kept in a growth chamber with conditions identical to those used with the leaf discs ($25 \pm 2°C$, $80 \pm 5\%$ RH, and a photoperiod of 16:8 [L:D] h). After 1 d, one egg was left on each leaf, and the remaining eggs as well as the female were removed. A data logger (HOBO U12, Onset Computer Corporation, Bourne, MA) was placed inside a cup with a leaf and water tube as a control to record conditions inside the cups. The average relative humidity inside the cup was 10% higher than inside the growth chamber. The life history data were recorded as described for the leaf disc method. The whole leaves, with very few exceptions, maintained their condition for the duration of the life study. When necessary, wilting or desiccating leaves were replaced with new leaves.

Life Table Analysis. The life history raw data of all individuals were analyzed based on the age-stage, two-sex life table theory (Chi and Liu 1985) and the method described by Chi (1988). The age-stage specific survival rate (s_{xj}, where x = age and j = stage), age-stage specific fecundity (f_{xj}), age-specific survival rate (l_x), age-specific fecundity (m_x), life expectancy (e_{xj}) and reproductive value (v_{xj}), preoviposition period of female adult (APOP), and total preoviposition period of female counted from birth (TPOP) were calculated. The population parameters (r, intrinsic rate of increase; λ, finite rate of increase; R_0, net reproduction rate; and T, the mean generation time) were calculated as well. Intrinsic rate of increase was estimated by using the iterative bisection method from the Euler–Lotka formula:

Table 1. Life history statistics (mean ± SE) of *T. urticae* on leaf discs and whole leaves

Statistics	Leaf disc mean ± SE	Whole leaf mean ± SE	t	df	P
Developmental time					
Egg	3.68 ± 0.06	3.47 ± 0.10	1.88	119	0.630
Larva	1.45 ± 0.06	1.53 ± 0.08	0.70	111	0.487
Protonymph	1.33 ± 0.06	1.41 ± 0.09	0.69	90	0.493
Deutonymph	1.73 ± 0.06	1.22 ± 0.07	5.9	90	0.000
Total preadult duration	8.20 ± 0.09	7.60 ± 0.12	3.82	90	0.000
Adult longevity					
Female	3.83 ± 0.27	4.71 ± 0.42	1.81	62	0.076
Male	4.41 ± 0.64	5.09 ± 1.29	0.52	26	0.606
Preoviposition period					
APOP	0.89 ± 0.09	0.29 ± 0.10	4.29	54	0.000
TPOP	9.14 ± 0.14	7.81 ± 0.18	5.96	54	0.000
Lifetime fecundity	12.05 ± 2.78	22.81 ± 3.31	2.34	62	0.023

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

with age indexed from 0 (Goodman 1982). The life expectancy (e_{xj}) was calculated according to Chi and Su (2006). The mean generation time is defined as the period of time needed by a population to increase to R_0-fold of its size (i.e., $e^{rT} = R_0$ or $\lambda^T = R_0$) at the stable age-stage distribution and is calculated as $T = (\ln R_0)/r$. The means and standard errors of the life table parameters were estimated by using the Jackknife method (Sokal and Rohlf 1995). The computer program TWOSEX-MSChart (Chi 2005) was used for data analysis and Jackknife estimation. The program is available at http://140.120.197.173/Ecology and at http://nhsbig.inhs.uiuc.edu/wes/chi.html. The Student's *t*-test was used to determine differences in population parameters, developmental times, and fecundities between the leaf disc and whole leaf methods. To reveal the capability in describing the age-stage structure and the growth potential, we projected the population growth of *T. urticae* by using the computer program TIMING-MSChart (Chi 2006) based on the life table results. This program is also available at the above mentioned websites.

Results

There were significant differences in developmental times of deutonymph stage, total preadult duration, APOP and TPOP at the 95% confidence level (Table 1). The fecundity of mites reared on whole leaves was significantly higher than those reared on leaf discs. The relative number alive (s_{xj}), i.e., age-stage survival rate, gives the probability that a new born egg will survive to age x and stage j. Overlapping occurs between stages (Fig. 1). Values for the age-specific survival rate of total cohort (l_x), female age-specific fecundity (f_{x5}), age-specific fecundity of the total population (m_x) and age specific maternity ($l_x m_x$) are presented in Fig. 2. The reproduction periods were similar in both methods but occurred one day earlier in the whole leaf method. Reproductive peaks, how-
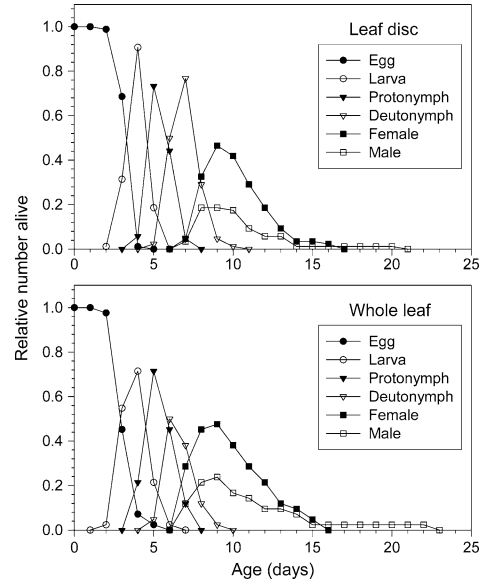

Fig. 1. Relative number alive in each age-stage group (s_{xj}) of *T. urticae* on leaf discs and whole leaves.

ever, occurred much earlier (day 9) on whole leaves than that on leaf discs (day 14). The life expectancy curve (e_{xj}) shows the total time that an individual of age x and stage j is expected to live (Fig. 3). The reproductive value (v_{xj}) gives the expectation of future offspring of individuals of age x and stage j (Fig. 4). The major peak in reproductive values of females occurred much earlier (day 8) in the whole leaf method ($v_{8,5} = 14.98$) than that for females reared on leaf discs (day 14, $v_{14,5} = 16.93$).
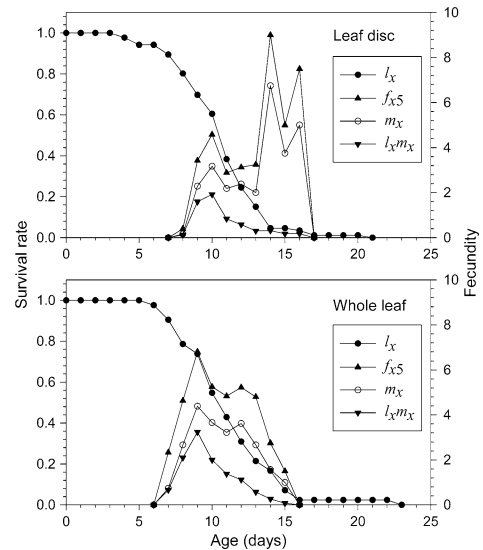

Fig. 2. Age-specific survival rate (l_x), female age-specific fecundity (f_{x5}), age-specific fecundity of the total population (m_x), and age-specific maternity ($l_x m_x$) of *T. urticae* on leaf discs and whole leaves.
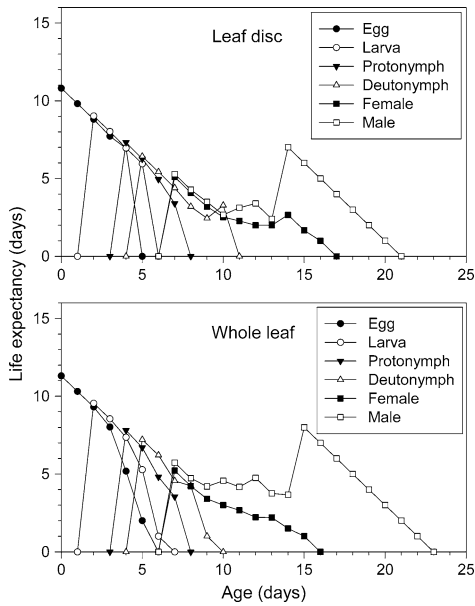
Fig. 3. Age-stage life expectancies (e_{xj}) of *T. urticae* on leaf discs and whole leaves.

The intrinsic rate of increase, finite rate of increase, and net reproductive rate were significantly higher when using the whole leaf method (Table 2). There were no significant differences in mean generation time. The number of female adults obtained by using population projection is plotted in Fig. 6. The population projection based on the life table using whole leaves results in a faster increase in the mite population.
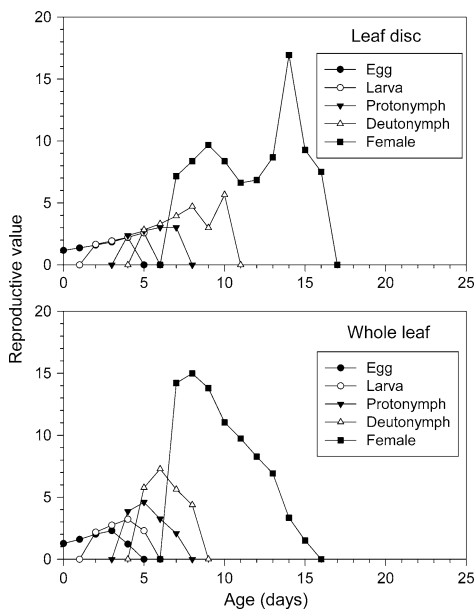

Fig. 4. Age-stage specific reproductive values (v_{xj}) of *T. urticae* on leaf discs and whole leaves.

Table 2. Mean ± SE of intrinsic rate of increase (r) (day^{-1}), finite rate of increase (λ) (day^{-1}), net reproductive rate (R_0) (offspring/individual), and mean generation time (T) of *T. urticae* on leaf discs and whole leaves

Pop parameter	Leaf disc mean ± SE	Whole leaf mean ± SE	t	df	P
r	0.159 ± 0.02	0.235 ± 0.03	2.31	126	0.022
λ	1.17 ± 0.02	1.26 ± 0.03	2.38	126	0.019
R_0	6.02 ± 1.53	11.40 ± 2.42	1.95	126	0.054
T	11.52 ± 0.44	10.45 ± 0.31	1.60	126	0.111

Discussion

The results of this study demonstrate some of the advantages of using the age-stage, two-sex life table theory in describing demography over the female-based age-specific life table. For example, the overlapping in curves of s_{xj} (Fig. 1) shows the potential of the age-stage, two-sex life table in revealing the stage differentiation of *T. urticae* due to the variable developmental rates among individuals. However, the l_x constructed based on a female age-specific life table (e.g., Fig. 1 of Martínez-Villar et al. 2005) ignores the differences among individuals and assumes all individuals have the same developmental period. This ignorance will lead to miscalculations in the survival and fecundity curves and some other problems (Chi 1988, Chi and Yang 2003, Yu et al. 2005). Similarly, the stage differentiation can be observed in the e_{xj} and v_{xj} curves (Figs. 3 and 4). Moreover, survival rates and life expectancies of male adults would have not been included if a female age-specific life table were used. The earlier peak of v_{xj} shows that *T. urticae* population can increase faster on whole leaves than that on leaf discs. The advantages of age-stage, two-sex life table have been discussed in detail by Chi (1988), Yu et al. (2005), and Chi and Su (2006). The two-sex life table was applied to the aphid, *Therioaphis maculate* (Buckton) (Homoptera: Aphididae) by Silva et al. (2006), and to the midge, *Feltiella acarisuga* (Vallot) (Diptera: Cecidomyiidae) by Mo and Liu (2006).

Our results demonstrated that there were significant differences in both the developmental time and reproductive potential between *T. urticae* reared on leaf discs and those reared on whole leaves (Table 1). These differences consequently result in significant differences in population parameters (Table 2). Because most whole leaves lasted longer than 3 wk after being cut from the bean plants, they were not replaced during the life table study. In some test units, we observed that new roots regenerated from the petioles of the whole leaves inserted in the water tubes. It is reasonable to hypothesize that whole leaves have better nutritive value than leaf discs, resulting in the higher intrinsic rate of increase. Few studies have focused on the effects of nutritional quality of host plants on development of *T. urticae*. For example, Wermelinger et al. (1991) demonstrated the negative effect of nitrogen and phosphorus deficiencies on population growth of *T. urticae*. Because leaf discs are widely used in many studies, we suggest that addi-

The reproductive value v_{xj} gives the contribution of an individual of age x and stage j to the future population. The value v_{01} is exactly the finite rate and it is the contribution a newborn will make to the growth of population at SASD (stable age-stage distribution). At SASD, an egg will increase to 1.26 eggs after one day. The value v_{75} gives the contribution of a female of age 7 to the future population is 14.2. It is much higher than v_{01}, because a female of age 7 will not suffer the mortality from egg to adult. It can immediately produce offspring and thus contribute to the population growth at a higher rate.
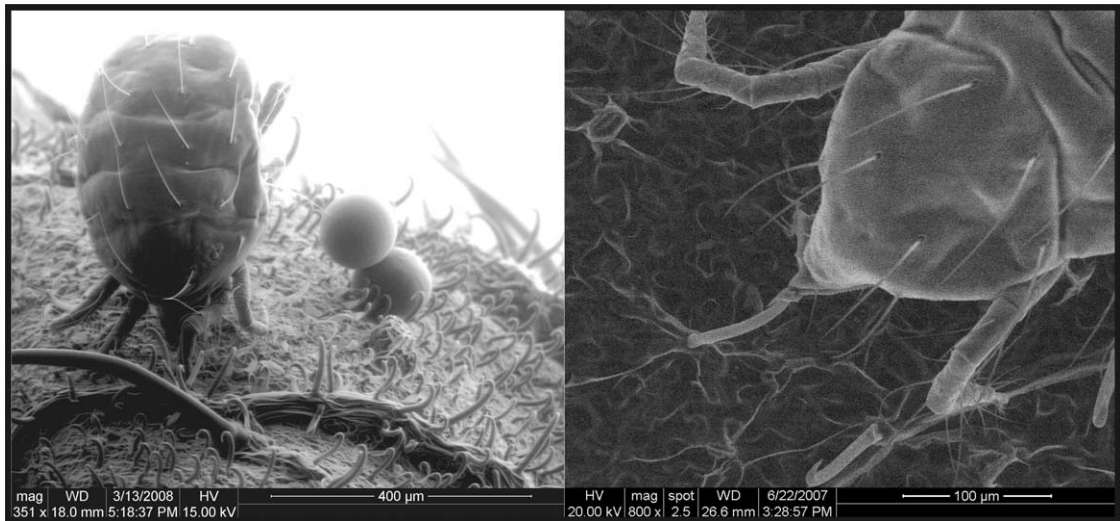
Fig. 5. Scanning electron microscope pictures showing a mite trapped in a jungle of hooks (left) and the posterior part of a mite entrapped by a leaf trichome (right).

tional studies are urgently needed comparing the nutritional contents of leaf discs and whole leaves.

The developmental times and intrinsic rates of *T. urticae* found in our study are consistent with some published studies using bean plants as host. Praslička and Huszár (2004) reported a preadult duration of 8.20 d at 25°C. Fang and Chi (1989) reported the developmental duration for each preadult stage as 3.8, 1.7, 1.5, and 1.7 d for egg, larva, protonymph, and deutonymph, respectively. At 27°C and 90% RH, Shih et al. (1976) observed shorter developmental times for egg (2.3 d), larva (0.6 d), and protonymph stages (0.4 d) but longer duration for deutonymph stage (1.9 d) than our results. Conversely, Kasap (2002) reported much longer total preadult durations of 10.9 d at 25°C and 60% RH. Bounfour and Tanigoshi (2001) reported a longer preadult development of 13.9 d on raspberry at 25°C. Differences in published data may be due to differences in host plants, temperature, and rearing methods. The main differences between our results and similar studies are seen in longevity of adults and lifetime fecundity. The short longevity observed in both males and females occurred because of special characteristics found in the variety of bean plant used. Based on our observations, the mites (mainly adults and, rarely, deutonymphs) were often entrapped by hooked trichomes found on the lower surface of the leaf, leading to their death within 1–3 d (Fig. 5). This was also the main cause of the low lifetime fecundity. Similar observations have been reported by Fang and Chi (1989). Leaf hairs (both glandular and nonglandular) have been reported as a morphological defense mechanism entrapping the mites by van den Boom et al. (2003). Tobacco, strawberry and tomato are other plants species that have previously been reported to possess similar characteristics (van den Boom et al. 2003, Gassmann and Hare 2005). In spite of this, the intrinsic rate of increase in our studies using whole leaves (0.235) was in the range commonly reported (0.219–0.336; Sabelis 1991). The intrinsic rate of increase on leaf discs (0.159), however, was below this range. The shortened total preadult developmental time, so that the total preoviposition period (TPOP), together with the higher fecundity occurring on whole leaves compensate for the negative effects of the trichomes. Despite the presence of the deleterious trichomes, *T. urticae* readily survives on the plant under cultivated conditions and remains a major pest of bean with a high intrinsic rate of increase. The population projection based on the age-stage, two-sex life table gives detailed stage structures of *T. urticae* (Fig. 6). If the female only life table was used, the stage differentiation would not have been observed. Because the number of female adults is generally used in economic threshold and injury level calculations, the capability of revealing stage structure based on the age-stage, two-sex life table can be useful in pest management strategies.

In conclusion, age-stage, two-sex life tables provide a more comprehensive insight into the stage differentiation of *T. urticae* than do the traditional female age-specific life table. In addition, we conclude that using whole leaves produces more realistic life table data than using the traditional leaf discs because whole leaves deteriorate much slower than do leaf discs, and, therefore, maintain a higher nutritional quality. The intrinsic rates of increase for *T. urticae* has been reported by Sabelis (1991) to range from 0.219 to 0.336. However, the development, fecundity and consequently the population parameters depend on many factors, e.g., temperature (Wermelinger et al. 1990, Krips et al. 1998, Bounfour and Tanigoshi 2001, Praslička and Huszár 2004), humidity (Boudreaux 1958), and host plant (Skirvin and Williams 1999, van den Boom et al. 2003, Praslička and Huszár 2004). In future studies, the demographic data for *T. urticae* reared on whole leaves of
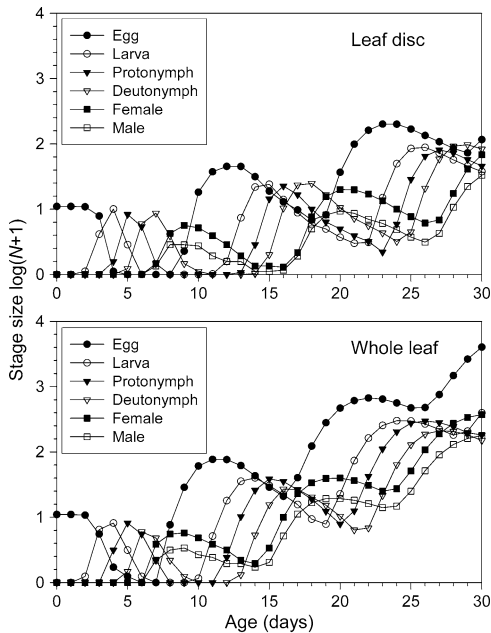
Fig. 6. Population projection of *T. urticae* from an initial population of 10 eggs.

different host plants should be collected for use in diverse pest management strategies.

Acknowledgments

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