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Adult movements and population dynamics of two bamboo aphids (*Hemiptera: Aphididae*)

Abstract - The paper deals with the development, parametrization and validation of models that represent the dynamics of age-structured *Takecallis arundinariae* (Essig) and *T. taiwanus* (Takahashi) populations on bamboo. These models are based on the matrices of Leslie (1945) and Lefkowitch (1965) and explain the observed infestation patterns on the basis of temperature effects on development, fecundity and survival. A key role is given to the movements of adults between the bamboo plot under study and the surroundings. Previously published observations and experiments carried out in the nursery are used for both parameter estimation and validation of the model, which satisfactorily represents the observed infestation patterns, indicates limitations (the developmental rate is linearly related to the temperature) and shows the possibilities for extending the study to the whole year.

Riassunto - *Movimento degli adulti e dinamica di popolazione di afidi del bamboo (Hemiptera: Aphididae)*

Il lavoro riguarda lo sviluppo, la parametrizzazione e la validazione di modelli che rappresentano la dinamica di popolazione di *Takecallis arundinariae* (Essig) e *T. taiwanus* (Takahashi) su bambù. Questi modelli sono basati sulle matrici di Leslie (1945) e Lefkovitch (1965) e spiegano l'infestazione osservata sulla base dell'effetto della temperatura su sviluppo, fecondità e sopravvivenza. Viene assegnato un ruolo chiave ai movimenti degli adulti tra la parcella di bambù sotto studio e l'ambiente circostante. Osservazioni precedentemente pubblicate ed esperimenti condotti in vivaio sono stati usati per la stima dei parametri e per la validazione del modello, che fornisce una rappresentazione soddisfacente dell'infestazione osservata, indica dei limiti (il tasso di sviluppo è linearmente legato alla temperatura) e mostra la possibilità di estendere lo studio all'intero anno.

Key words *Takecallis arundinariae*, *Takecallis taiwanus,* bamboo, matrix model, temperature effects, movement

INTRODUCTION

Takecallis arundinariae (Essig) and *T. taiwanus* (Takahashi) are the most widespread aphids in lombardic bamboo nurseries (Limonta et al., 2002). Both aphids are of oriental origin and live on leaves of *Arundinaria* and *Phyllostachys* bamboo (Blackman & Eastop, 1994). The plants of the two bamboo genera are native to monsoon climate regions (Maoyi, 1998) and susceptible to drought and dry air (Scurlock *et al.*, 2000). *Phyllostachys* is also cultivated in temperate climates and grows within an optimum temperature interval of 20–26 °C. *P. bambusoides* is known to be very resistant to cold winter conditions and to develop at temperatures above a threshold situated below 0°C (Chao, 1998).

During three years, Limonta *et al.* (2002) made observations in a nursery where *P. bambusoides* was grown. They obtained information on life tables, recorded the population fluctuations of the two species and carried out experiments on age-specific fecundity and mortality rates. In a first attempt to explain the observed infestation patterns, a key role was attributed to temperature. The importance given to aphid movements (e.g. Liu, 1994; Wilson, 1995; Blackman & Eastop, 2000; Woiwood *et al.*, 2001; West-Eberhard, 2003; Braendle *et al.*, 2006) and the re-examination of the data obtained by Limonta et al. (2002) suggest that this process might also have played an important role in the dynamics of the two aphids.

The purpose of this paper is to improve the understanding of the dynamics of *T. arundinariae* and *T. taiwanus* populations inhabiting the bamboo plot. This is achieved by the development and use of models appropriate for representing the dynamics of age-structured populations poikilothermic populations (Di Cola *et al.*, 1999).

MATERIALS AND METHODS

Data acquisition

In 1998, 1999 and 2000, observations on population fluctuations and life table studies were carried out in a 400 m^2 lot in a nursery located at Mariano Comense, CO (Italy). There, two years old *P. bambusoides* Siebold & Zuccarini, cultivar "Castillonis" was grown. In each year, the field observations were conducted from February to July for *Takecallis arundinariae* and from May to August for *T. taiwanus*.

The aphids under study predominantly inhabit the apical part of the plant (Qiao & Zhang, 2004). At the beginning of each year, one shoot on each of ten different plants was randomly selected. Once selected, the shoots were kept for sampling purposes during the remaining observation period. The sampling unit on each shoot consisted of three extended leaves and the curled apical leaf. The population fluctuations were observed through weekly visual counts of adults and nymphs. Only few natural enemies including some ladybirds (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae), gall gnats (Diptera: Cecyiidomidae) and hoverflies (Diptera: Syrphidae) have been observed towards the end of the growing season. Their impact during the main infestation period was considered as negligible and hence, they are not taken into account in this analysis.

Model description

The model represents the dynamics of poikilothermic populations and hence, should take into account temperature influences on development and demographic processes (Gilbert *et al.*, 1976). The observations by Limonta *et al.* (2002) have shown that the observed populations display time varying age structures, i.e. the proportion of nymphs to adults changes through time. Hence, the model should be able to represent the dynamics of age-structured populations (Di Cola *et al.*, 1999).

Limonta *et al.* (2002) presented the dynamics of populations consisting of young aphids, nymphs and adults. To overcome the difficulties of separating the immature aphids into two groups, we combine the young aphids and the nymphs into one stage referred to as "nymphs".

The Leslie version of the matrix model described by Leslie (1945), Wang *et al.* (1977), Caswell (1989), Di Cola *et al.* (1999) and Bommarco (2001) is used to represent the dynamics of the two aphid populations

$$n(t+\Delta t)=A(t)n(t) \qquad [1a]$$

where $n(t)$ and $n(t+\Delta t)$ are the densities at time t and $(t+\Delta t)$, respectively, and $\boldsymbol{A}(t)$ is the transition matrix detailed below. In our work, we rely on Leftkovitch's (1965) version of the matrix model.

Age and time are expressed as physiological variables, as to take into account the effect of the temperature on poikilotherms development (Gilbert *et al.*, 1976; Di Cola *et al.*, 1999). We assume that the developmental rates of the two species are linearly related to the effective temperatures expressed in degrees above a lower threshold temperature below that no development occurs. The daily mean temperatures have been obtained from figures 1 and 2 in the publication of Limonta *et al.* (2002).

With reference to the total development (Table 1), we divide the individual development into 45 and 40 sub-stages for *T. arundinariae* and for *T. taiwanus*, respectively, and obtain the species-specific time increments Δt equal to 15.7 and 27 day degrees [dd]. Eq. 1a is detailed by

$$\begin{bmatrix} n_1 \\ n_2 \\ \cdots \\ \cdots \\ n_q \end{bmatrix}_{t+1} = \begin{bmatrix} n_1 \\ n_2 \\ \cdots \\ \cdots \\ n_q \end{bmatrix}_{t} \begin{bmatrix} m_1 & m_2 & \cdots & \cdots & m_q \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & P_{q-1} & 0 \end{bmatrix}_{t} \qquad [1b]$$

where n_i $(i=1, 2,...q)$ is the density of individuals in the i^{th} sub-stage, m_i $(i=1, 2,...q)$ is the sub-stage specific fecundity rate, and P_i $(i=1, 2,...q-1)$ represents the sub-stage specific probability of survival (Birch, 1948). In this work, we use a Microsoft ® Excel 2000

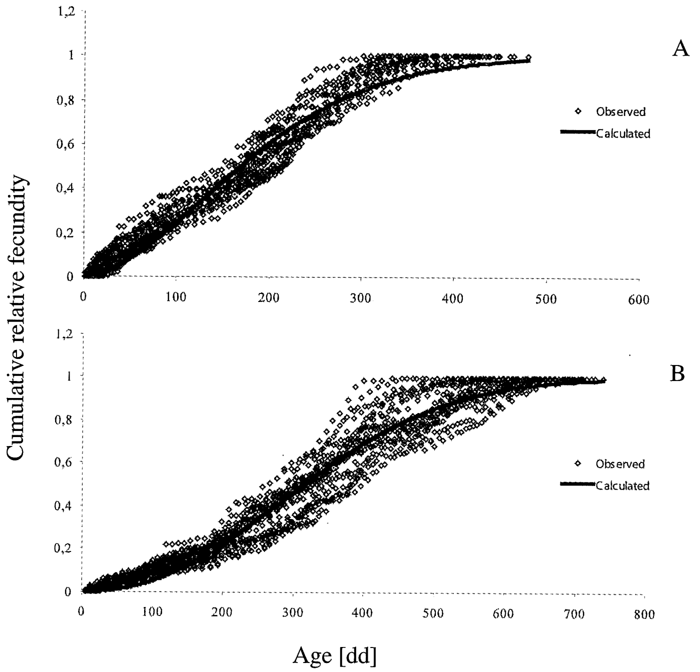

Fig. 1 - Observed and predicted cumulative relative fecundity of adults of T. arundinariae (A) for 1998 and 2000, and of T. taiwanus (B) for 1998, 1999, 2000; physiological age is expressed in units of day degrees [dd].

version of Lefkovitch's (1965) matrix model adapted by Jungck & Spangenberg (2005). The finite rate of increase λ is calculated as the factor of population increase during Δt once the stable stage structure distribution has been reached (Jungck & Spangenberg, 2005). The model has been implemented on the Microsoft ® Excel spreadsheet program operating in a Microsoft ® Visual Basic 6.0 environment and modified to take into account the adult movements.

Parameter estimation

Thresholds

The thresholds are reported in Table 1. In the case of *T. arundinariae*, the developmental threshold has been derived from observations reported in the literature (Coffelt & Shultz, 1990; Limonta *et al.*, 2002). In the case of *T. taiwanus*, the developmental threshold has been obtained as an average from the life stage specific thresholds reported by Xu *et al.* (2003).

Table 1 - Developmental thresholds and durations of nymphal and adult life stages of *Takecallis arundinariae* and *T. taiwanus*; physiological age is expressed in units of day degrees [dd].

Species	**Threshold [°C]**	**Duration [dd]**	
		Nymphs	Adults*
T. arundinariae	3	211.61	494.575
T. taiwanus	8.7	330.43	752.36

*: maximum lifespan observed in the field.

Life table parameters

In each of the three years under study, developmental time, fecundity and mortality were studied on 30 randomly selected plants. On each plant, one leaf was put into a cylindrical transparent polyester cage with the length of 10 cm and the diameter of 3.5 cm (see Limonta *et al.*, 2002). A single nymph ready to moult into the adult stage was introduced into the cage. Daily, the number of living adults and their progeny production was recorded, and the newly born nymphs were removed from the cage. The cage was removed and the observations were terminated after the death of the adults. For each year, the proportions of living adults and the cumulative proportions of nymphs produced were plotted against physiological age. For *T. taiwanus* the studies undertaken during the three years were considered, while only the data obtained in 1998 and 2000 were used for *T. arundinariae*.

Fecundity

The cumulative age-specific fecundity *r(x)*, relative to the total fecundity, is represented by a modified function proposed by Bieri *et al.* (1983)

$$r(x)=1-e^{\left(-a_1 \cdot x^{a_2}\right)} \qquad [2]$$

The age of adults x is expressed in units of day degrees [dd]. The parameters a_1, a_2, are estimated by least square regression techniques, and their values are reported in Table 2; the comparison between observed and calculated fecundity is presented in fig. 1.

The specific fecundity rate m_i (eq. 1b) for the *i-th* sub-stage is calculated as follows. The age of adults is subdivided into 32 and 28 sub-stages for *T. arundinariae* and *T. taiwanus*, respectively; subsequently, m_i is calculated by multiplying the sub-stage specific fecundity rate with the total fecundity of the two species (Fig. 2; Table 2); m_i is positive for adults and equal to zero for nymphs ($i < 14$ for *T. arundinariae* and $i < 13$ for *T. taiwanus*).

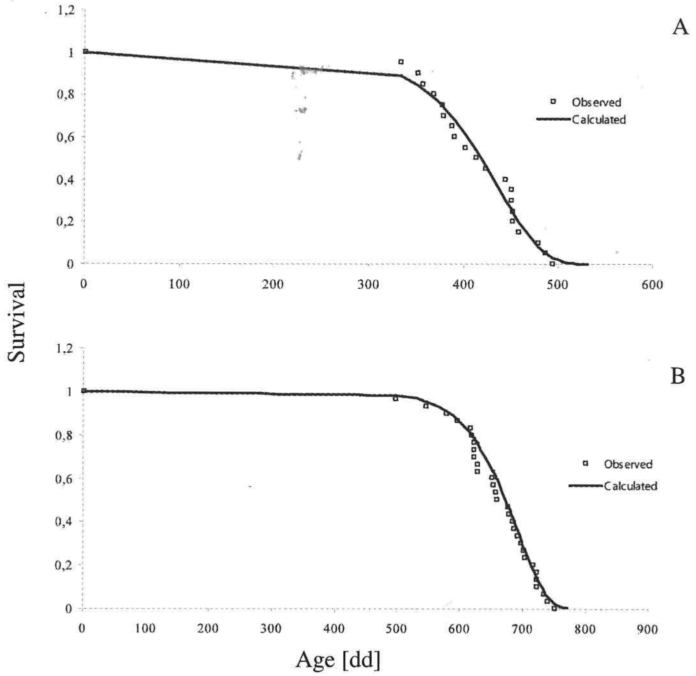

Fig. 2 - Observed and predicted survival of adults of *T. arundinariae* (A) for 1998 and 2000, and of *T. taiwanus* (B) for 1998, 1999, 2000; physiological age is expressed in units of day degrees [dd].

Table 2 - Values of the estimated parameters of the age specific fecundity and survival function (eq. 2, 3, 4b, 4c), and the total fecundity obtained from Limonta *et al.* (2002).

Species	**Fecundity**		**Total fecundity (mean ± SE)**	**Survival**				
	a_1	**a_2**		μ	**b_1**	**b_2**	**c_1**	**c_2**
Takecallis arundinariae	2.055E-04	1.61	105.7±4.15	0.625	1.84E-05	0.025	0.024	17
Takecallis taiwanus	1.87E-06	2.23	151.4±2.72		5.1E-07	0.021	0.018	20

Mortality and movements

Nymphal survival. In absence of data on nymphal mortality for the two species, the intrinsic survival of nymphs is obtained from readily available data on six different aphid species observed under constant environmental conditions (Bieri *et al.*, 1983; Graf *et* *al.*, 1985; Harrington *et al.*, 1995; Kairo & Murphy, 1999; Kersting *et al.*, 1999; Wang & Tsai, 2000; Tong-Xian Liu & Bisong Yue, 2001; Tsai & Wang, 2001; Hafiz, 2002; Satar & Yokomi, 2002; Bayhan *et al.*, 2005; Kuo *et al.*, 2006; Mehrparvar & Hatami, 2007). From these studies, we obtain an average immature mortality $\sigma = 0.2$. For the field conditions under study, we add an extrinsic mortality μ representing other mortality factors than temperature, and obtain the probability of nymphal survival (eq. 3)

$$P_i = (1-\sigma)\cdot(1-\mu) \qquad \text{for } i = 1, 2, \ldots, 13 \ (T.\ arundinariae) \qquad [3]$$
$$\text{for } i = 1, 2, \ldots, 12 \ (T.\ taiwanus)$$

The value for μ has been obtained by seeking a correspondence between model predictions and observations, and is reported in Table 2.

Adult survival. We assume that the movement of the adults is restricted to the first third of the adult sub-stages. The population loss is composed of the intrinsic mortality and the net losses ($1 - z_i(t)$) due to movements of aphids leaving the bamboo plantation. Thus, the overall sub-stage-specific probability P_i of survival is

$$P_i(t) = s_i z_i(t) \qquad \text{for } i = 14, 15, \ldots, 45 \ (\text{for } T.\ arundinariae) \qquad [4a]$$
$$\text{for } i = 13, 14, \ldots, 40 \ (\text{for } T.\ taiwanus)$$

The sub-stage specific intrinsic probability s_i of adult survival is calculated as follows. First, the probability of intrinsic survival $v(x)$ is represented by a modified Gompertz function (Strehler, 1977)

$$v(x) = e^{\left(-b_1 \cdot e^{(b_2 \cdot x)}\right)} \qquad [4b]$$

where the parameters b_1, b_2 have been estimated by least square regression techniques. The values are reported in Table 2, while observed and calculated intrinsic survival for both species are depicted in fig. 2. Next, the age (x) of adults is subdivided into 32 and 28 sub-stages of lengths equal to 502.4 dd and 756 dd for *T. arundinariae* and *T. taiwanus*, respectively. Subsequently, s_i is obtained by calculating the relative proportion of surviving individuals within each sub-stage. The multiplication with the sub-stage specific probability $z_i(t)$ corrects the population density for the losses due to net movements

$$z_i(t) = e^{-c_1\left(\frac{t}{\Delta t} - c_2\right)} \qquad \text{for } i = 14, 15, \ldots, 24 \ (\text{for } T.\ arundinariae) \qquad [4c]$$
$$\text{for } i = 13, 14, \ldots, 21 \ (\text{for } T.\ taiwanus)$$

$$z_i(t) = 1 \qquad \text{for } i > 24 \ (\text{for } T.\ arundinariae) \qquad [4d]$$
$$\text{for } i > 21 \ (\text{for } T.\ taiwanus)$$

The parameters c_1, c_2 have been approximated by seeking a correspondence between model predictions and the observations in the two (for *T. arundinariae)* and three *(*for *T. taiwanus)* years under study. The values are reported in Table 2.

Nymphal development duration and adult life span

There are no data available on the duration of the nymphal period for the two species. As in the case of nymphal survival, the readily available literature on other aphids was consulted (Kersting *et al.*, 1999; Wang & Tsai, 2000; Tong-Xian Liu & Bisong Yue, 2001; Tsai & Wang, 2001; Satar & Yokomi, 2002; Bayhan *et al.*, 2005), and the duration has been obtained from the relationship between the nymphal development and the mean adult life span. The mean proportion of 0.52 indicates that the duration of the nymphal stages is about half of the adult lifespan.

Model initialization and validation

For each year and species, the initial numbers of nymphs and adults have been obtained from unpublished raw data summarized by Limonta *et al.* (2002) and reported in Table 3. The numbers of individuals in each sub-stage is obtained by dividing the initial number by the number of sub-stages in each life stage. For validation purposes the model predictions and the field observations are compared in fig. 3.

Tab. 3 - Initial numbers of nymphs and adults in the two years of study.

Species	**1998**		**2000**	
	Nymphs	**Adults**	**Nymphs**	**Adults**
Takecallis arundinariae	193	57	130	47
Takecallis taiwanus	170	33	199	48

Tab. 4 - The finite rate of increase of bamboo aphid populations (Takecallis arundinariae and T. taiwanus) for the two years under study,

Year	*T. arundinariae*	*T. taiwanus*
1998	1.0856	1.1004
2001	1.0882	1.1039

RESULTS

The two aphid species have different life spans. According to Table 1, *T. taiwanus* lives longer and has a longer reproductive period expressed in physiological time units. The total fecundity is also higher for this species than for *T. taiwanus*. Table 1 also reports the developmental thresholds of 3 °C for *T. arundinariae* and 8.7 °C for *T. taiwanus*. The duration of the nymphal development is 211.61 dd and 330.43 dd, while the duration of the adult stage is 494.575 dd and 752.36 dd for *T. arundinariae* and *T. taiwanus*, respectively.

The reproductive period is 479.25 dd for *T. arundinariae* and 739.9 dd for *T.*

taiwanus. Limonta *et al.* (2002) studied the total number of progeny produced by an individual and reported 105.7±4.15 and 151.4±2.72 for *T. arundinariae* and *T. taiwanus* respectively (Table 2).

Fig. 2 depicts the observed and predicted survival of adults for the three years under study. The modified Gompertz function appears to satisfactorily represent the observed data. The parameter a_2 (Table 2) results higher for *T. taiwanus* and generates a more flattened curve for this species than for *T. arundinariae*.

The finite rate of increase λ, between 1.0856 and 1.0882 for *T. arundinariae* and between 1.1004 and 1.1039 for *T. taiwanus,* is a measure for the increase of the populations during the time increment.

The model adequately represents the poikilothermic nature of the populations under study and the time varying age structure of the populations. Figure 3 shows the predicted

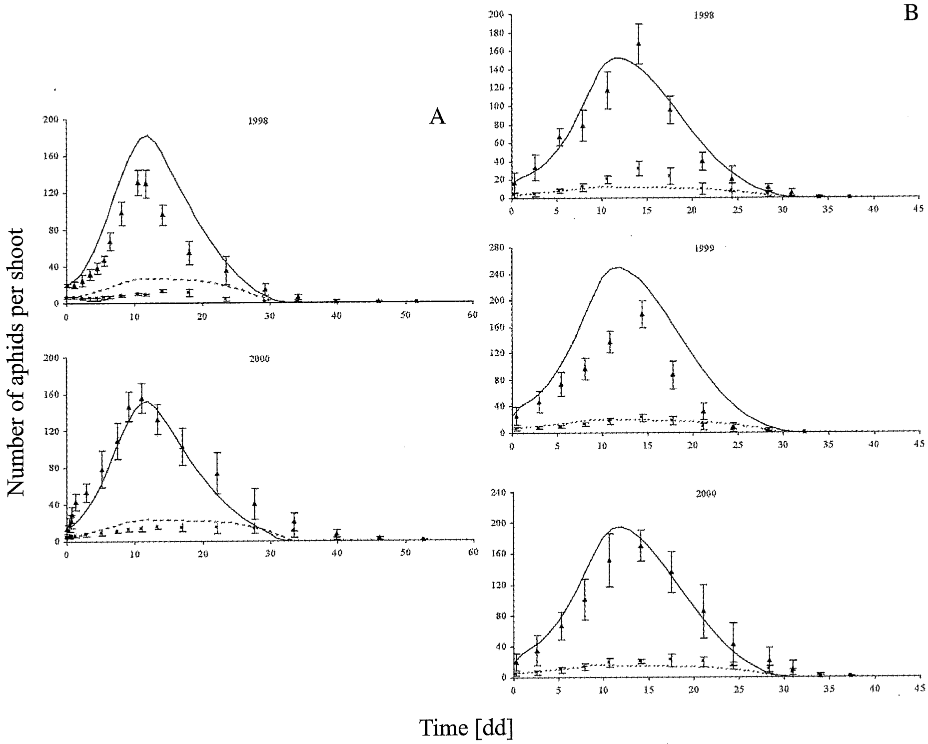

Fig. 3 - Predicted and observed population fluctuations of *Takecallis arundinariae* (A) in 1998, 2000 and of *T. taiwanus* (B) in 1998, 1999, 2000. The continuous lines represent the predicted nymphs fluctuations, the dotted lines are the adult's fluctuations, triangles are the observed mean densities of the nymphs and squares are the observed mean densities of the adults. The vertical bars represent the standard errors; physiological time is expressed in units of day degrees [dd].

and the observed fluctuations for the two species in the years under study. The predictions by a model without movement are not depicted but would lead to an exponential increase in population densities. According to Figure 3, there is a close agreement between observed and predicted data.

DISCUSSION AND CONCLUSIONS

Early in 1999, there was a series of unusual consecutive drops in daily mean temperatures from about 10°C to temperatures close to 0 °C. These drops occurred during the observed populations fluctuations of *T. arundinariae*, while the beginning of the observations on *T. taiwanus* started about one month later. Hence, these drops are more likely to have affected, during the observational period, the fluctuations of *T. arundinariae* than of *T. taiwanus*. However, the life table studies of the former species have been carried out immediately after these drops. Nevertheless, the observed mean adult life span of *T. arundinariae* was 869 day degrees in 1999 as opposed to 430 day degrees in 1998 and 404 day degrees in 2000, whereas there was no such an effect on *T. taiwanus* development. Since it is difficult, in our view, to relate such a delay to the previous drop in temperature, we refrain from calibrating the model and from representing the dynamics of *T. arundinariae* in 1999. We suggest to experimentally verify the temperature threshold and investigate this effect in future work.

The lower developmental threshold of *Takecallis taiwanus* is higher than the one of *T. arundinariae*, while the bamboo host plant has a much lower threshold (Chao, 1989; Scurlock *et al.*, 2000). Hence, at the relatively low temperatures during winter and spring, the bamboo species may provide suitable conditions for the development of both aphids. *T. arundinariae* has a lower threshold than *T. taiwanus* and hence, is able to respond earlier to increasing temperatures. This difference appears in the observed infestation patterns (Fig. 1 in Limonta *et al.*, 2002). There is no information on upper thresholds for the two aphid species under study. This is not a serious limitation for this study, however, because the main period of aphid fluctuations on bamboo in the nursery under observation falls into a relatively cool period from February to June. In absence of conflicting information, we consider the linear developmental rate – temperature function as adequate for the period under study. From about mid June, however, the increasing temperatures may exceed the temperature range in which the linear model is applicable and require both the consideration of a non-linear model and a thorough revision of the population model developed in this work.

The model (eq. 1a) is based on fecundity and mortality rates that are specific to the sub-stage of the aphids but are constant through physiological time during the observation period. It predicts an exponential increase of the population density. However, this kind of population dynamic has not been observed in the field (Limonta *et al.*, 2002). The observed infestation patterns, however, can be represented by the consideration of the adult movements between the bamboo plot under study and the surroundings.

Hence, these movements turn out to be the key factor in the population dynamics of the two species.

In physiological time units, *T. taiwanus* lives longer, has a longer reproductive period and a higher fecundity than *T. arundinariae*. The life table statistics of the two species can be summarized in the finite rate of increase (Birch, 1948). Lefkovitch's (1965) model with constant parameters (fecundity and survival) and a positive growth rate results in a geometrical increase of the population that eventually reaches a stable stage distribution. In this case, dividing a predicted number with the one obtained in the current time interval can approximate the finite rates of increase for the two species. The values reported in Table 4 are higher for *T. taiwanus* than for *T. arundinariae* and increase during the years of observation. Apparently, the conditions for aphid population development have improved during the years under study. The specific definition of the time increment renders difficult a comparison with published finite rates of increase of other aphids. Therefore, we refrain from drawing conclusions regarding the calculated rates with respect to other species.

The previous studies have shown that the current effect of natural enemies on the dynamics of the two aphid population is negligible (Limonta *et al.*, 2002). This corresponds to the result of many studies where natural enemies of aphids were unsuccessful in preventing aphid outbreaks. Occasionally, however, natural enemies can reduce the rate of increase of aphids (Dixon, 1985). Additional studies are considered as a prerequisite for increasing the number of natural enemies and rely on them in aphid population management.

The model attributes a key role to the movement of adults and satisfactorily represents the observed infestation patterns in the bamboo plot on the basis of temperature influences on development, fecundity and survival. Nevertheless, the purpose of the model was not the representation of the population dynamics throughout the year. This can only be achieved by extending the period of observations and including studies on aphid population development in the surroundings of the bamboo plots.

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REFERENCES

BAYHAN E., ÖLMEZ-BAIHAN S., ULUSOY M.R., BROWN J.K., 2005 - Effect of temperature on the biology of *Aphis punicae* (Passerini) (Homoptera: Aphididae) on pomegranate. Environ. Entomol. 34 (1), 22-26.

BIERI M., BAUMGÄRTNER J., BIANCHI G., VON ARX R., 1983 - Development and fecundity of pea aphid (*Acyrthosiphon pisum* Harris) as affected by constant temperatures and by pea varieties. Mitt. Schweiz. Entomol. Ges. 56, 163-171.

BIRCH L.C., 1948 - The intrinsic rate of natural increase of an insect population. J. Animal Ecol. 17(1), 15-26.

BLACKMAN R.L., EASTOP V.F., 1994 - Aphids on the world's trees. An identification and information guide. CAB International, Wallingford, Oxfordshire, UK, 904 pp.

BLACKMAN R.L., EASTOP V.F., 2000 - Aphids on the world's crops. An identification and information guide. Wiley, Chichester, UK, 466 pp.

BOMMARCO R., 2001 - Using matrix models to explore the influence of temperature on population growth of arthropod pests. Agric. Forest Entomol. 3, 275-283.

BRAENDLE C., DAVIS G.K., BRISSON J.A., STERN D.L., 2006 - Wing dimorphism in aphid. Heredity 97, 192-199.

CASWELL H., 1989 - Matrix population models. Sinauer, Sunderland, USA, 722 pp.

CHAO C.S., 1998 - A guide to bamboos grown in Britain. Royal Botanic Gardens, Kew, UK, 47 pp.

COFFELT M.A., SCHULTZ P.B., 1990 - Seasonal abundance and population dynamics of a bamboo aphid, *Takecallis arundinaria* (Homoptera: Aphididae). J. Entomol. Sci. 25 (4), 526-534.

DI COLA G., GILIOLI G., BAUMGÄRTNER J., 1999 - Mathematical models for age-structured population dynamics. In Huffaker C.B. and Gutierrez A.P. (eds): Ecological Entomology. 2nd ed. Wiley, New York, USA, pp. 503-534.

DIXON A.F.G., 1985 - Aphid Ecology. Blackie, Glasgow, UK, 157 pp.

GILBERT N., GUTIERREZ A.P., FRAZER B.D., JONES R.E., 1976 - Ecological relationships. Freeman, Reading, UK, 156 pp.

GRAF B., BAUMGÄRTNER J., DELUCCHI V., 1985 - Life table statistics of three apple aphids, *Dysaphis plantaginea*, *Rhopalosiphum insertum*, and *Aphis pomi* (Homoptera, Aphididae), at constant temperatures. Z. angew. entomol. 99, 285-294.

HAFIZ ALI N.A., 2002 - Effects of certain cucumber varieties on the biology of *Aphis gossypii* (Homoptera: Aphididae). 17th Symposium of the International Farming Systems Association, November 17-20, Lake Buena Vista, Florida USA.

HARRINGTON R., BALE J.S., TATCHELL G.M., 1995 - Aphids in a changing climate. In: Harrington R. and Stork N.E. (eds): Insects in a changing environment. Academic Press, London, UK, pp. 134-135.

JOHNSON B., 1957 - Studies on the degeneration of the flight muscles of alate aphids. I. A comparative study of the occurrence of muscle breakdown in relation to reproduction in several species. J. Insect Physiol. 1, 248-256.

Jungck R. & Spangenberg J.A., 2005 - Leslie/Lefkovitch matrix models for age or stage-structured populations 1.0 [http://www.bioquest.org/esteem/esteem_details.php?product_id=210] [retrieved on November 26, 2007).

Kairo M.T.K., Murphy S.T., 1999 - Temperature and plant nutrient effects on the development, survival and reproduction of *Cinara* sp. nov., an invasive pest of cypress trees in Africa. Ent. Exp. Appl. 92, 147-156.

Kersting U., Satar S., Uygun N., 1999 - Effect of temperature on development rate and fecundity of apterous *Aphis gossypii* Glover (Hom., Aphididae) reared on *Gossypium hirsutum* L. J. Appl. Ent. 123, 23-27.

Kring J.B., 1972 - Flight behaviour of aphids. Annu. Rev. Entomol. 17, 461-492.

Kuo M.H., Lu W.N., Chiu M.C., Kuo Y.H., Hwang S.H., 2006 - Temperature-dependent development and population growth of *Tetraneura nigriabdominalis* (Homoptera: Pemphigidae) on three host plants. J. Econ. Entomol. 99 (4), 1209-1213.

Lefkovitch L.P., 1965 - The study of population growth in organisms grouped by stages. Biometrics 21, 1-18.

Leslie P.H., 1945 - On the use of matrices in certain population mathematics. Biometrika 33, 183-212.

Limonta L., Colombo M., Redaelli A., 2002 - Field observations on *Takecallis arundinariae* (Essig) and *T. taiwanus* (Takahashi). Boll. Zool. agr. Bachic. Ser. II. 34 (3), 397-404.

Liu S.S., 1994 - Production of alatae in response to low temperature in aphids: a trait of seasonal adaptation. In Danks H.V. (eds.): Insect life-cycle polymorphism: Theory, evolution and ecological consequences for seasonality and diapause control. Kluwer Academic Publishers, Dordrecht, NL, pp. 245-261.

Maoyi F., 1998 - Bamboo resources and utilization in China. In: Kumnming and Xishuangbanna (eds): Proceedings of the Workshop "Bamboo conservation, diversity, ecogeography, germplasm, resource utilization and taxonomy". Yunnan, China, 10-17 May.

Mehrparvar M., Hatami B., 2007 - Effect of temperature on some biological parameters of an Iranian population of the rose aphid, *Macrosiphum rosae* (Hemiptera: Aphididae). Eur. J. Entomol. 104, 631-634.

Moericke V., 1955 - Über die Lebensgewohnheiten der geflügelten Blattläuse (unter besonderer Berücksichtigung des Verhaltens beim Landen). Z. angew. Entomol. 37, 29-91.

Qiao G-X, Zhang G-X, 2004 - Review of the genus *Takecallis* Matsumura (Homoptera: Aphididae: Myzocallidinae) from China and description of one new species. The Raffles Bulletin of Zoology, 52 (2): 373-378.

Satar S., Yokomi R., 2002 - Effect of temperature and host on development of *Brachycaudus schwartzi* (Homoptera: Aphididae). Ann. Entomol. Soc. Am. 95 (5), 597-602.

Scurlock J.M.O., Dayton D.C. Hames B., 2000 - Bamboo: an overlooked biomass resource? Biomass and Bioenergy 19 (4), 229-244.

Strehler B.L., 1977 - Time, cells and, aging, VI. Ultimate effects of cellular aging. In: VI. Ultimate effects of cellular aging-mortality - A review of theories of mortality. 2nd ed. Academic, New York, pp. 103-125.

Tong-Xian Liu and Bisong Yue, 2001 - Comparison of some life history parameters between alate and apterous forms of turnip aphid (Homoptera: Aphididae) on cabbage under constant temperatures. Fla. Entomol. 84 (2), 239-242.

Tsai J.H., Wang J.J., 2001 - Effects of host plants on biology and life table parameters of *Aphis spiraecola* (Homoptera: Aphididae). Environ. Entomol. 30 (1), 44-50.

Wang Y., Gutierrez A.P., Oster G., Daxl R., 1977 - A population model for plant growth and development: coupling cotton-herbivore interaction. Can. Entomol. 109, 1359-1374.

WANG J.J., TSAI J.H., 2000 - Effect of temperature on the biology of *Aphis spiraecola* (Homoptera: Aphididae). Ann. Entomol. Soc. Am. 93 (4), 874-883.

WEST-EBERHARD M.J., 2003 - Developmental plasticity and evolution. Oxford University Press, Oxford, UK, 820 pp.

WILSON K., 1995 - Insect migration in heterogeneous environments. In: Drake V.A. and Gatehouse A.G.: Insect migration: Tracking Resources through space and time. Cambridge University Press, Cambridge, UK, pp. 243-264.

WOIWOOD I.P., REYNOLDS D.R., THOMAS C.D., 2001 - Insect movement: mechanisms and consequences. CABI Publishing, Wallingford, Oxfordshire, UK, pp. 1-18.

XU H.C., SHI Z.H., HONG W., 2003 - Low development threshold temperature and effective thermal constants of *Takecallis taiwanus* (Takahashi) (Homoptera: Callaphididae). J. Zhejiang Forestry College. 20 (4), 385-388.

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