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A matrix model for predicting seasonal fluctuations in field populations of *Paronychiurus kimi* (Collembola: Onychiruidae)

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Abstract

A matrix model for the population dynamics of *Paronychiurus kimi* in the field, based on life table statistics of *P. kimi* in a laboratory at constant temperature under optimum environmental conditions is described. The temperature-dependent development and fertility schedule of *P. kimi* were estimated in terms of degree-days (for temperatures ≥ 7.83 °C). The model simulates reasonably accurately the seasonal fluctuation of *P. kimi* in Ichon, Korea. It predicted a significantly higher density than that observed in the field between mid April and early June, when the soil moisture content was lowest and with high variance. Our results suggest that soil moisture content is the limiting factor suppressing the population below the density level predicted. The validity of the model as a standard phenology of *P. kimi* in the field is discussed, including the capability to account for factors other than temperature.

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Keywords: Stage-structured matrix; Temperature-dependent development; Degree-days; *Paronychiurus kimi*; Population dynamics; Simulation

1. Introduction

Soil Collembola are an important component of soil fauna (Al-Assiuty and Khalil, 1996), and have been used as test organisms in ecotoxicological studies in soil (Frampton, 1997). However, the role of Collembola as test organisms is reliable only if their population ecology and genetics are understood in relation to the biotic and abiotic components of the soil environment.

The population dynamics of Collembola are complex, involving ecological characteristics such as seasonal changes and communal behaviour (Usher, 1970;

Bödvarsson, 1973; Vegter, 1987; Ponge et al., 1993). Abiotic and biotic factors including soil temperature, soil moisture content, soil porosity and nutrient content, and microbial biomass, all influence populations of Collembola (Hopkin, 1997). The population ecology of Collembola can be understood only through integrated studies of all these factors. However, the concealed nature of Collembola in soil, and the complexity of the soil ecosystem, have restricted study of the actions and interactions of these factors. Simulation of a collembolan population using a simplified but realistic model might, therefore, clarify the interaction of factors that govern field populations.

Longstaff (1977) reported that laboratory population dynamics of *Onychiurus armatus* Bagnall and *Hypogastrua denticulata* Handschin were described accurately by the Leslie matrix model. However, a

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population model at a constant temperature is unable to simulate the population dynamics of *Collembola* in the field, since the soil temperature fluctuates daily and seasonally.

It is well known that insect development rate depends on temperature, and can be estimated on the basis of heat accumulation (degree-days). Demographic analyses based on degree-days give good predictability for populations in changing temperature conditions (Ryoo et al., 1988) and in the field (Jones et al., 1997). We, therefore, assume that a stage-structured matrix model (Lefkovich matrix; see Caswell, 2001; Jensen, 1995) based on degree-days gives an accurate simulation of collembolan populations in the field. Bommarco (2001) analyzed the factors influencing population growth of four arthropod pests using a stage-structured matrix model on the basis of degree-days. However, the applicability of the model to field population dynamics under fluctuating temperatures was not considered.

The present study sets up a matrix model for the population dynamics of *Paronychiurus kimi* (Lee) on the basis of degree-days, and tests the resulting simulations against a field population, which was measured periodically in a rice paddy field in Ichon, Korea in 1998. *P. kimi* is the dominant species in the area (Kang et al., 2001).

2. Materials and methods

2.1. Field study site and monitoring environmental factors

Our field population of *P. kimi* was located in Anhung-Dong, Ichon, Korea (37°3' N, 127°4' E). The climate is hot and wet in summer, and cold and dry in winter. The temperature varied from –16.5 to 31.7°C with an annual average of 12.1°C, and the total precipitation for 1998 was 1803 mm. The main crop is rice. Soybean was also planted, along part of the field embankment.

The soil temperature at the sample site was measured using immediate action thermometers (Technoterm® 7300, Testoterm Inc.). The temperature was read 1 min after inserting the sensor into the soil to a depth of 3 cm.

The moisture content of the soil was measured as follows (Okoh et al., 1999). About 5 g of soil was extracted from each sample, weighed accurately (CT 1200-K, Ohaus), heated in an oven at $105 \pm 2^\circ\text{C}$ for 24 h, cooled and re-weighed. The moisture content was estimated from the formula:

$$\text{moisture content (\%)} = \frac{(W_W - D_W)}{D_W} \times 100 \quad (1)$$

where W_W and D_W are the weights of the soil sample before and after heating.

To estimate the organic matter content of the soil, we ground the dried samples with a laboratory mill so as to pass through 0.5 mm mesh, and measured the total carbon content using the Tyurin method (Nelson and Sommers, 1996).

Fig. 4 shows the soil temperature and soil moisture content recorded in 1998, and Fig. 5 shows the total soil organic matter (SOM) content in 1998.

2.2. Soil sampling and *P. kimi* extraction

P. kimi in soil were sampled using a core sampler (diameter 6 cm) and collection of top soil to a depth of 5 cm every other week from March to November 1998. A total of 30 soil samples were collected from the embankment. These samples were placed in polythene bags, and the mouth of the bag was tied to prevent the soil drying. Collembola were extracted from the soil samples in a laboratory over 14 days using a modified high gradient extractor (Crossley and Blair, 1991).

3. Stage-structured matrix model

3.1. The matrix model

To describe the population dynamics of *P. kimi*, we categorized the population into three biologically defined stages: eggs, juveniles, and adults. The adult stage was not further divided into reproductive and post-reproductive stages because too few adults in the post-reproductive phase were caught in the field.

The model is of the form:

$$\mathbf{n}(t + 1) = \mathbf{A}(t)\mathbf{n}(t) \quad (2)$$

where $\mathbf{n}(t)$ is a vector giving the numbers of the population in each stage at time t , and $\mathbf{A}(t)$ is a popula-

tion projection matrix (Caswell, 2001). The discrete projection interval (from t to $t+1$) is 1 day. The age structure vector representing the population at time t is

$$\mathbf{n}(t) = \begin{bmatrix} n_e(t) \\ n_j(t) \\ n_a(t) \end{bmatrix} \quad (3)$$

where $n_e(t)$, $n_j(t)$, and $n_a(t)$, respectively, denote the numbers of eggs, juveniles, and adults at time t . The projection matrix $A(t)$ takes the form

$$A(t) = \begin{bmatrix} P_e(t) & 0 & N_e(t) \\ U_j(t) & P_j(t) & 0 \\ 0 & U_a(t) & P_a(t) \end{bmatrix} \quad (4)$$

where $N_e(t)$ is the average number of eggs produced per day per individual, and $U_j(t)$ and $U_a(t)$ are the transition probabilities to juveniles and adults, respectively. Here $P_e(t)$, $P_j(t)$, and $P_a(t)$ are the probabilities of eggs, juveniles, and adults remaining in the same stage of development within a unit period.

The data needed to describe the development and egg production of *P. kimi* at different temperatures were taken from the study by Choi et al. (2002).

3.2. Transition probabilities based on degree-days

The transition probabilities per day were estimated using the concept of degree-days. The degree-day (DD) parameter in this study is defined as:

$$\begin{aligned} \Delta t &= (t + 1) - t, \\ DD(t) &= 0, & \text{if } T_{\text{mean}}(t) \leq T_L \\ DD(t) &= (T_{\text{mean}}(t) - T_L)\Delta t, & \text{if } T_{\text{mean}}(t) > T_L \end{aligned} \quad (5)$$

where t is the time (day), $T_{\text{mean}}(t)$ is daily average temperature, and T_L is the lower threshold temperature for development (Hochberg et al., 1986).

The degree-day parameter was estimated from the mean daily soil surface temperature in the Ichon area according to the Korea Meteorological Administration.

The probabilities for staying in the same stage of development (P_i) and the probabilities for advancement to the next stage (U_i) are estimated, using the cumulative Weibull distribution function (Wagner et al., 1984), as:

$$U_i(t) = \left(\frac{G_i(t) - G_i(t-1)}{1 - G_i(t-1)} \right) \quad (6)$$

$$P_e(t) = 1 - U_j(t) \text{ and } P_j(t) = 1 - U_a(t) \quad (7)$$

$$G_i(t) = 1 - \exp \left[- \left(\frac{DD(t) + c_i(\ln 2)^{1/d_i} - b_i}{c_i} \right)^{d_i} \right] \quad (8)$$

where subscript i indicates each developmental stage (e: egg; j: juvenile; and a: adult), $G_i(t)$ is cumulative developmental rate of each stage, b_i , c_i , and d_i are the cumulative Weibull function parameters, and $DD(t)$ is the cumulative degree-day number at time t .

The probability of remaining as an adult (P_a) in a unit time period was taken as constant and was estimated on the basis of the field data collected in 1998: 0.8 for temperatures above 25 °C, and 0.9 when the temperature is less than 25 °C.

3.3. Per day fertility of *P. kimi*

The fertility in relation to degree-days was well described by the Weibull function (Fig. 1B), but could not be estimated due to inhibition of the oviposition at higher temperatures than optimum (around 25 °C; Fig. 2). We estimated the number of eggs produced per day using the Logan/Lactin model (Lactin et al., 1995), which describes the number of eggs per day as:

$$N_e(t) = e^{\alpha T} - e^{[\alpha T_{\text{max}} - (T_{\text{max}} - T)/\beta]} + \gamma \quad (9)$$

where $N_e(t)$ is the temperature-dependent fertility (eggs/day); T the temperature; and α , β , γ , and T_{max} are fitting parameters. This model permits the estimation of the lower (T_L) and upper (T_U) temperature thresholds, and the optimum temperature (T_O) for oviposition.

3.4. Limiting of population increase by environmental resistance

The effect of biotic factors on increase in the collembolan population (Longstaff, 1977) is taken to depend on the total population through the density-dependent fertility (Choi et al., 2002). It can, therefore, be modeled by multiplying the fertility rate by a function $\varphi(k)$ which depends on the population size, defined as

$$\begin{aligned} \varphi(k) &= ((1 - k)/k_{\text{max}}) & \text{for } k < k_{\text{max}} \\ \varphi(k) &= 0 & \text{for } k \geq k_{\text{max}} \end{aligned} \quad (10)$$

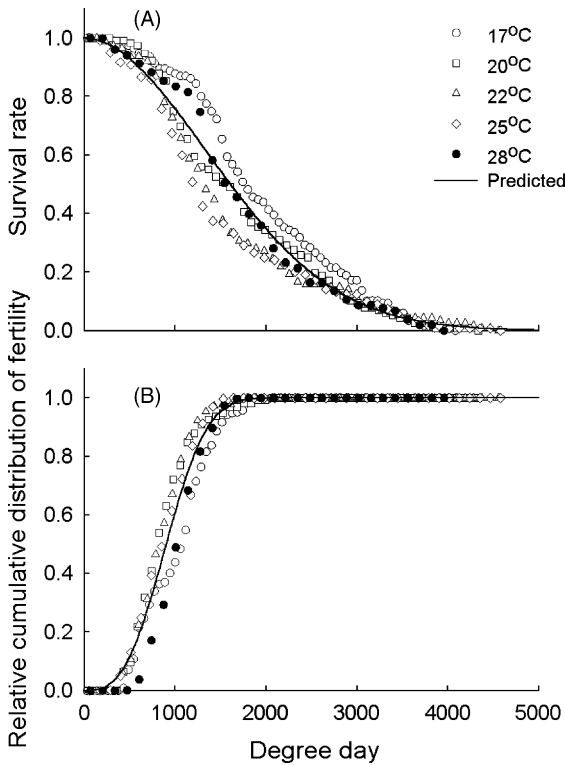


Fig. 1. Survival rate (A) and cumulative relative fertility (B) curves of *P. kimi* at five different temperatures vs. degree-day. The survival rate and the cumulative fertility are $y = \exp(-(x/1946.18)^{1.93})$ (Pinder et al., 1978) and $y = 1 - \exp(-(x/1023.04)^{2.93})$ (Johnson and Kotz, 1970), where y is the rate and x is degree-day.

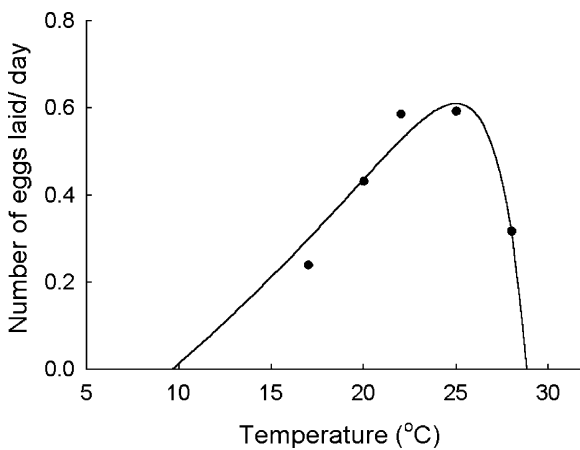


Fig. 2. Relation between temperature and daily fertility of *P. kimi*. Circles and the solid line respectively indicate observed values and values predicted by Lactin's equation.

where k is the population size (number of juveniles + adults)/sample core and k_{\max} is the carrying capacity/sample core. Here, k_{\max} is empirically determined as 50 per sample core on the basis of the density of the field population surveyed in 1998. We have incorporated the function $\varphi(k)$ into our extended matrix model.

3.5. The goodness-of-fit test of the model

The predictive power of the model for the field population was estimated using the coefficient of determination (r^2) of the regression of the density observed on the density predicted, indicating the proportion of the collembolan density variation explained by the model, and the χ^2 -test (Zar, 1999).

4. Results and discussion

Fig. 1 shows that the survival rate and the relative fertility rate curves at five different temperatures can all be described by a single equation based on degree-days. This result verifies that the effect of varying temperature can be accounted for by transforming the calendar date into degree-days, as suggested by Ryoo et al. (1998) and Jones et al. (1997).

Fig. 2 shows that egg production of *P. kimi* is dependent on the daily temperature, fitting the Logan/Lactin model well (Table 1). The lower, upper, and optimum temperatures for *P. kimi* oviposition were estimated as 8.85, 28.79, and 25.00 °C.

Table 1 shows estimates of the parameters in the functions of the matrix model.

Table 1
Parameter values for the relation between DD and life history of *P. kimi*

Cumulative development rate (Model)	Parameters			r^{2a}	
	b	c	d		
Egg to juvenile	154.10	247.79	15.00	0.89	
Juvenile to adult	490.52	101.36	3.23	0.99	
	α	β	γ	T_{\max}	
Temperature-dependent egg production per day	0.027	1.62	-1.27	30.32	0.96

^a r^2 is the amount of variation explained by the given equation.

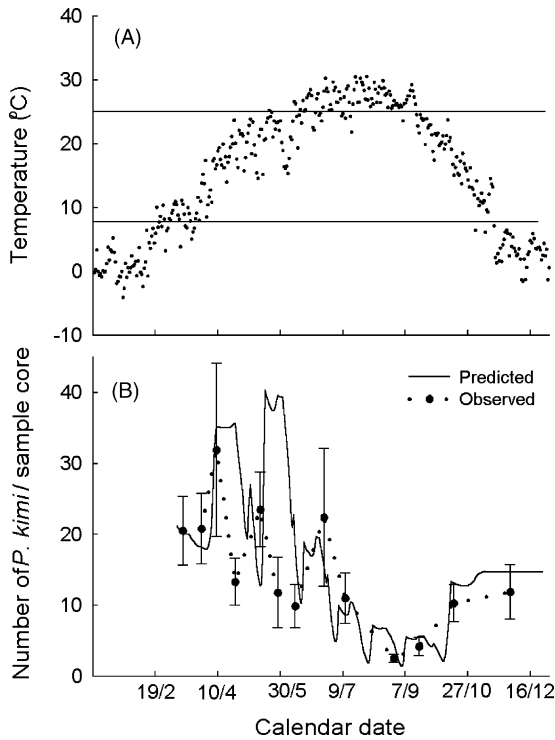


Fig. 3. Seasonal changes in (A) surface soil temperature and (B) observed density of *P. kimi* population (circles), and density predicted by matrix model (solid line), in the paddy field in Ichon in 1998. The two horizontal lines indicate the lower threshold (7.83 °C) and optimum temperature (25.00 °C) for reproduction of *P. kimi*.

The density of *P. kimi* predicted by the matrix model shows similar trends to the field population, except in mid April, and early June ($r^2 = 0.79$; Fig. 3). We constructed the model on the basis of the demography of a population maintained at optimum environmental conditions in our laboratory (Choi et al., 2002). The failure of the model in predicting suppression of the population density in mid April and early June is most likely due to environmental factors not considered in the model.

Herbicides and pesticides were intensively applied for pest control on this survey site during the test periods. This would affect the *P. kimi* population in the field both directly and indirectly. Herbicide application removed weed coverage of the soil (personal observation) and enhanced water evaporation from the soil, reducing the soil moisture content and thereby

suppressing the field population of *P. kimi*. As illustrated in Fig. 4, the intervals of low population density occurred when the soil moisture content was low and was highly variable. Choi et al. (2002) observed that reproduction of *P. kimi* was suppressed when the soil moisture content fell below 20%. Badejo and Lasebikan (1996) and Crouau et al. (1999) found the soil moisture content to be an important factor in Collembola population dynamics.

Pesticide application could also induce dispersal of *P. kimi*, which are repelled by the chemicals (Badejo and Adejuyigbe, 1994), so that a lower number of Collembola are observed. A direct impact of pesticides on collembolans in agricultural soil has been observed (Diekkrüger and Röske, 1995).

The quantity of total SOM was similar around the year, so that this is only a minor factor (Fig. 5).

The present results suggest that field populations with complex environmental factors are reasonably simulated by a stage structure matrix model constructed from a population maintained in a laboratory in a simple and optimum environment. The model has great potential in elucidating the major limiting factor in the field population, which is difficult to analyse because of concealed nature of Collembola in soil and the complexity of the soil ecosystem.

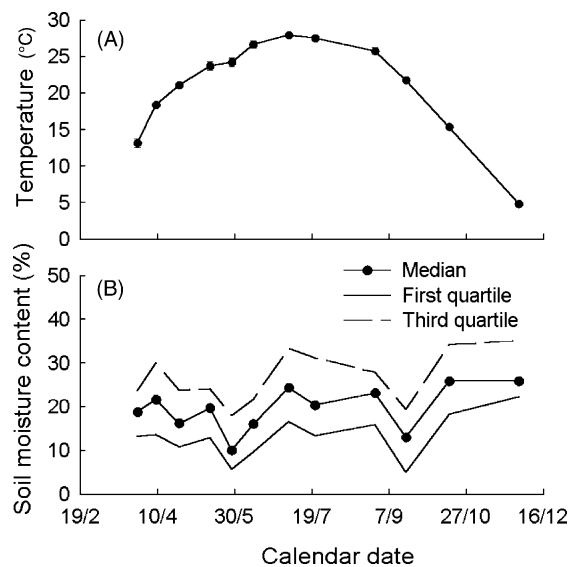


Fig. 4. Seasonal changes in SOM observed in the survey area located in Ichon, Kyonggi-Province in 1998.

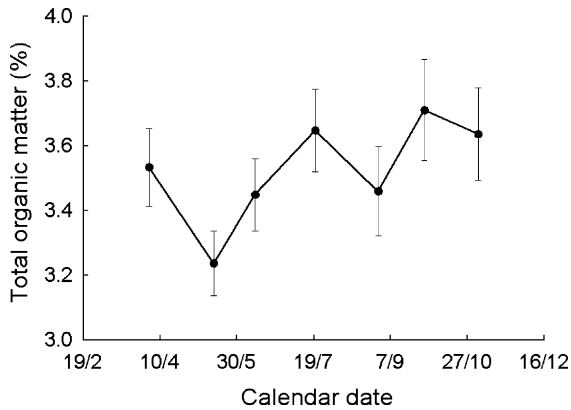


Fig. 5. Seasonal changes in SOM content observed in the survey area located in Ichon, Kyonggi-Province in 1998.

5. Conclusion

The present stage-structured matrix model suggests that the effect of varying temperatures on the field population can be accounted for by using degree-day instead of calendar date. This stage-structured matrix model can be compared with the population realized in the field to estimate its parameters. It is helpful in detecting limiting factors of population development, and constructing more sophisticated models. Our results suggest that soil moisture content is the limiting factor suppressing the *P. kimi* population. Studies of the interaction between temperature and other environmental factors, such as soil moisture content, could improve the utility of the present model.

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References

Al-Assiuty, A.I.M., Khalil, M.A., 1996. Effects of the herbicide atrazine on *Entomobrya musatica* (Collembola) in field and laboratory experiments. *Appl. Soil Ecol.* 4, 139–146.

Badejo, M.A., Adejuyigbe, T.A., 1994. Influence of hexazinone on soil microarthropods in Nigeria. *Fresenius Environ. Bull.* 3, 263–268.

Badejo, M.A., Lasebikan, B.A., 1996. Effects of habitat disturbances on the Collembola populations of a cassava plantation in Ile-Ife, Nigeria. *Fresenius Environ. Bull.* 5, 258–263.

Bödvarsson, H., 1973. Contribution to the knowledge of Swedish forest Collembola, with note on seasonal variation and alimentary habits. Royal College of Forestry, Stockholm, Institute of Forest Zoology. Research Note. 13, 43 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.

Caswell, H., 2001. *Matrix Population Models*. Sinauer Associates, Sunderland.

Choi, W.I., Ryoo, M.I., Kim, J., 2002. Biology of *Paronychiurus kimi* (Collembola: Onychiuridae) under the influences of temperature. *Pedobiologia* 46, 548–557.

Crossley Jr., D.A., Blair, J.M., 1991. A high-efficiency, “low-technology” Tullgren-type extractor for soil microarthropods. *Agric. Ecosyst. Environ.* 34, 187–192.

Crouau, Y., Chenon, P., Gisclard, C., 1999. The use of *Folsomia candida* (Collembola: Isotomidae) for the bioassay of xenobiotic substances and soil pollutants. *Appl. Soil Ecol.* 12, 103–111.

Dieckkrüger, B., Röske, H., 1995. Modelling the population dynamics of *Isotoma notabilis* (Collembola) on sites of different agricultural usage. *Pedobiologia* 39, 58–73.

Frampton, G.K., 1997. The potential of Collembola as indicators of pesticide usage: evidence and methods from the UK arable ecosystem. *Pedobiologia* 41, 161–168.

Hochberg, M.E., Pickering, J., Getz, W.M., 1986. Evaluation of phenology models using field data: case study for the pea aphid, *Acyrtosiphon kondoi* (Homoptera: Aphididae). *Environ. Entomol.* 15, 65–87.

Hopkin, S.P., 1997. *Biology of Springtails*. Oxford University Press, Oxford.

Jensen, A.L., 1995. Simple density-dependent matrix model for population projection. *Ecol. Model.* 77, 43–48.

Johnson, N.L., Kotz, S., 1970. *Distributions in Statistics: Continuous Univariate Distributions-1*. Houghton Mifflin Co., Boston.

Jones, V.P., Tome, C.H.M., Caprio, L.C., 1997. Life tables for the koa seedworm (Lepidoptera: Tortricidae) based on degree-day demography. *Environ. Entomol.* 26, 1291–1298.

Kang, S.Y., Choi, W.I., Ryoo, M.I., 2001. Demography of *Paronychiurus kimi* (Lee) population (Collembola: Onychiuridae) under the influence of glufosinate-ammonium on plaster charcoal substrate and artificial soil. *Appl. Soil Ecol.* 18, 39–45.

Lactin, D.J., Holliday, N.J., Johnson, D.L., Craigen, R., 1995. Improved rate model of temperature-dependent development by arthropods. *Environ. Entomol.* 24, 68–75.

Longstaff, B.C., 1977. The dynamics of Collembola populations: a matrix model of single species population growth. *Can. J. Zool.* 55, 314–324.

Nelson, D.W., Sommers, L.E., 1996. Total carbon, organic carbon, and organic matter. In: Bartels, J.M. (Ed.), *Methods of Soil Analysis. Part 3: Chemical Methods*. Soil Science Society of America, Inc. and American Society of Agronomy, Inc., Madison.

- Okoh, I.A., Badejo, M.A., Nathaniel, I.T., Tian, G., 1999. Studies on the bacteria, fungi and springtails (Collembola) of an agroforestry arboretum in Nigeria. *Pedobiologia* 43, 18–27.
- Pinder III, J.E., Wiener, J.G., Smith, M.H., 1978. The Weibull distribution: a new method of summarizing survivorship data. *Ecology* 59, 175–179.
- Ponge, J.F., Arpin, P., Vannier, G., 1993. Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. *Eur. J. Soil Biol.* 29, 141–153.
- Ryoo, M.I., Cho, K.J., Yoo, C.K., 1988. Life table statistics of the rice weevil, *Sitophilus oryzae* (Coleoptera: Curculionidae) on the degree day scale. *Korean J. Appl. Entomol.* 27, 14–20.
- Usher, M.B., 1970. Seasonal and vertical distribution of a population of soil arthropods: Collembola. *Pedobiologia* 10, 224–236.
- Vegter, J.J., 1987. Phenology and seasonal resource partitioning in forest Collembola. *Oikos* 48, 175–185.
- Wagner, T.L., Wu, H.-I., Sharpe, P.J.H., Coulson, R.N., 1984. Modeling distributions of insect development time: a literature review and application of the Weibull function. *Ann. Entomol. Soc. Am.* 77, 475–487.
- Zar, J.H., 1999. *Biostatistical Analysis*. Prentice-Hall, New Jersey.