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## A modeling study of soil temperature and moisture effects on population dynamics of *Paronychiurus kimi* (Collembola: Onychiuridae)

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**Abstract** The effect of soil moisture on population dynamics of *Paronychiurus kimi* (Collembola) was examined by combining an empirical soil moisture model with a temperature-sensitive, stage-structured population model. Field observations of soil temperature were used to drive the population model, and simulations were compared to field observations of juvenile and adult densities. Simulations without soil moisture effects produced stable, inter-year population dynamics and a significant correlation between simulations and observations ( $n=12$ ,  $r^2=0.40$ ,  $P<0.05$ ) but overestimated densities during much of the year. Adding responses to soil moisture improved the fit between simulations and observations ( $n=13$ ,  $r^2=0.40$ ), suggesting that soil moisture is a major limiting factor on field populations of *P. kimi*. Moreover, an observed temporary decline in field populations during spring could be explained partly by the effects of an herbicide, paraquat (*N,N'*-dimethyl- $\gamma,\gamma'$ -bipyridylum dichloride) ( $r^2=0.45$ ), suggesting that paraquat imposes additional limits on collembolan populations.

**Keywords** Herbicide · *Paronychiurus kimi* · Population dynamics · Soil moisture · Stage-structured model

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### Introduction

Microarthropods play a number of roles in soil processes such as decomposition, nutrient cycling, and energy flow, although their direct contributions are often subtle (Seastedt 1984; Hunt et al. 1987; Hunter et al. 2003). Moreover, environmental factors such as temperature, soil moisture, and pH commonly affect the biology of soil microarthropods (van Gestel and van Diepen 1997; Choi et al. 2002; Cassagne et al. 2003; Ke et al. 2004), and are thus likely to have both direct and indirect impacts on soil systems (Reth et al. 2005). Because the responses of microarthropods to environmental factors are often nonlinear and can fluctuate across seasons, it is difficult to extrapolate the net effect of fluctuating environmental controls on microarthropods. Thus, insight to their impacts on soils requires a detailed assessment of temporal patterns of microarthropod responses to changing environmental conditions.

Collembola are among the most common, abundant, and ubiquitous groups of soil microarthropods. Temperature and moisture are two of the most important environmental factors affecting populations of soil-dwelling Collembola. In general, collembolan development and reproduction are so strongly regulated by temperature (Choi et al. 2002) that population dynamics have often been related to simple indexes of heat accumulation (Diekkrüger and Röske 1995; Choi and Ryoo 2003). In contrast, soil moisture is also a limiting factor for Collembola but is often overlooked. For example, Choi et al. (2002) found that reproduction, but not survival, of *Paronychiurus kimi* (Lee) was inhibited by low moisture in a laboratory study. van Gestel and van Diepen (1997) reported similar results for *Folsomia candida* (Willem). Both of these studies of soil moisture effects were conducted in laboratory mesocosms under constant temperature during short incubation periods (about 7 weeks), and we are unaware of any field studies demonstrating comparable results. However, a recent study of *P. kimi* populations in rice fields of Ichon, South Korea, also included both soil moisture and temperature regimes (Choi and Ryoo 2003). Herein, we use these data to ex-

amine responses of *P. kimi* populations to fluctuations in moisture and temperature under field conditions.

Mathematical models are useful tools to assess the effects of fluctuations in environmental factors on the dynamics of soil invertebrates such as nematodes (Moorhead et al. 1987, 2002) and Collembola (Dieckrüger and Röske 1995; Choi and Ryoo 2003). To date, most of these models have focused on temperature controls, with limited attention to moisture effects. However, Moorhead et al. (1987) and Weicht and Moorhead (2004) showed that moisture plays a substantial role in regulating population dynamics of nematodes in arid soils. We are aware of no model that has similarly examined the impacts of soil moisture on Collembola.

The aim of this study is to elucidate the combined effects of soil moisture and temperature controls on the population dynamics of *P. kimi*, a soil collembolan common to the Far East. To this end, we combine information from earlier experimental studies of this species (Choi et al. 2002; Choi and Ryoo 2003) with a stage-structured population-modeling approach that explicitly includes both temperature and moisture controls on soil invertebrates (Moorhead et al. 1987; Weicht and Moorhead 2004). Field observations of temperature and moisture drive this model, and observations of *P. kimi* population densities are used to validate model behavior.

## Materials and methods

### Field data

Choi and Ryoo (2003) examined the population dynamics of *P. kimi* under field conditions. These data consisted of field density of *P. kimi* and soil environmental factors such as temperature, soil moisture and soil organic matter content. The South Korean Meteorological Administration monitors soil temperature and precipitation for the region in which this site is located.

Soils were collected from the field site every 2–4 weeks in 1998 and 1999 (except for December–February). Soil moisture content was determined according to Okoh et al. (1999). In brief, about 5 g soil was weighed, dried in an oven at 105°C for 24 h, cooled, and reweighed. Moisture content was estimated from weight loss.

### Modeling population dynamics

Life-history data for *P. kimi* (Choi et al. 2002) provided parameters for use in a stage-structured population model (Moorhead et al. 1987), which was modified for application to this Collembola. This approach follows daily age cohorts of three life stages: eggs, juveniles, and adults (see below). Postreproductive stages of *P. kimi* were excluded because few individuals in this condition were collected in field samples (Choi and Ryoo 2003). Mortality, hatching,

and reproduction rates were controlled by soil temperature, according to the observations of Choi et al. (2002) and Choi and Ryoo (2003) for *P. kimi*, and information from studies of other related organisms (Longstaff 1977; Dieckrüger and Röske 1995).

### Development and longevity

Development rates of *P. kimi* are the reciprocals of the mean period (in days) needed to complete development of eggs and juveniles, respectively. The relationship between development rate ( $r$ ) and temperature ( $T$ ) is linear:

$$r_i = \rho_i(T - Tb_i), \quad (1)$$

where  $i$  is the life stage (e indicates egg and j, juvenile),  $\rho_i$  is slope, and  $Tb_i$  is the minimum temperature threshold for development. Parameter values are given in Table 1. We chose this simple linear model based on laboratory observations (Choi et al. 2002), and because field conditions do not exceed temperatures favorable for development.

The probabilities of remaining in the same stage of development ( $P_i$ ) or for advancing to the next stage ( $U_i$ ) are estimated using the cumulative Weibull distribution function (Dieckrüger and Röske 1995):

$$U_i = (G_{i,t} - G_{i,t-1}) / (1 - G_{i,t-1}), \quad (2)$$

$$P_e = 1 - U_j \text{ and } P_j = 1 - U_a, \quad (3)$$

and

$$G_i = 1 - \exp \left[ -(t_{bio})^{b_i} \right], \quad (4)$$

where  $i$  is the life stage (e, egg; j, juvenile; and a, adult),  $G_i$  is cumulative transition probability (0–1),  $t_{bio}$  is cumulative developmental status (0–1), and  $b_i$  is an empirical, best-fit parameter (Table 1).

### Reproduction

We estimate the number of eggs produced per day per individual using the Logan/Lactin model (Lactin et al. 1995):

$$N = \exp(\alpha T_u) - \exp[\alpha T_u - (T_u - T)/\beta] + \gamma, \quad (5)$$

where  $N$  is temperature-dependent fertility (eggs per day per female),  $T_u$  is the maximum temperature for egg production, and  $\alpha$ ,  $\beta$ , and  $\gamma$  are best-fit parameters (Table 1).

**Table 1** Parameter values for the model

Equation no.	Parameter	Definition	Unit	Value
1	$\rho_e$	Slope for egg development	Days	0.0058
	$\rho_j$	Slope for juvenile development	Days	0.0019
	$Tb_e$	Minimum temperature for egg development	°C	8.62
4	$Tb_j$	Minimum temperature for juvenile development	°C	7.01
	$b_i$	Exponent of egg and juvenile development	Unitless	7.00
5	$T_u$	Maximum temperature for egg production	°C	30.32
	$\alpha$	Best-fit parameter	Unitless	0.027
	$\beta$	Best-fit parameter	Unitless	1.62
	$\gamma$	Best-fit parameter	Unitless	-1.27
6	$k_{\max}$	Carrying capacity	Individuals	50.0
7	$S_e$	Maximum egg survival	Unitless	0.80
	$S_j$	Maximum juvenile survival	Unitless	0.99
9	$b_m$	Exponent of adult mortality	Unitless	7.00
10	$c_s$	Intercept for moisture effect on survival	Unitless	0.92
	$d_s$	Slope for moisture effect on survival	Unitless	0.0024
	$c_r$	Intercept for moisture effect on reproduction	Unitless	-0.0087
	$d_r$	Slope for moisture effect on reproduction	Unitless	0.026
12	$Q$	Constant for annual temperature regime	Unitless	15.36
	$U$	Amplitude for annual temperature regime	Unitless	-13.40
	$S$	Phase shift for annual temperature regime	Unitless	1.27
13	$M$	Intercept for temperature effect on soil moisture loss	Unitless	-0.014
	$N$	Slope for temperature effect on soil moisture loss	Unitless	4.64

We impose a density-dependent limitation to fertility in this model (Longstaff 1977) based on empirical observations of *P. kimi* (Choi et al. 2002). This effect ( $\varphi$ ) is a function of the population size:

$$\varphi = \begin{cases} ((1-k)/k_{\max}) & \text{for } k < k_{\max} \\ \varphi = 0 & \text{for } k \geq k_{\max}, \end{cases} \quad (6)$$

where  $k$  is the population size (density of juveniles + adults), and  $k_{\max}$  is the estimated carrying capacity, empirically defined as the maximum observed density of the field population surveyed in 1998 (Table 1).

#### Age-specific mortality

We use a general parabolic relationship to calculate development success ( $F_i$ ; fraction of eggs hatching and juveniles maturing) as a function of temperature (Moorhead et al. 1987):

$$F_i = S_i 4 (T - T_{\min})(T_{\max} - T) / (T_{\max} - T_{\min})^2, \quad (7)$$

where  $S_i$  is maximum cohort survival, and  $T_{\min}$  and  $T_{\max}$  are minimum and maximum temperatures for survival, respectively (Table 1).

Adult mortality  $M$  is age-dependent for Collembola, and so we estimate the probability for death ( $G_a$ ) at a given age with a Weibull function:

$$M = (G_{a,t} - G_{a,t-1}) / (1 - G_{a,t-1}) \quad (8)$$

and

$$G_a = 1 - \exp \left[ -(t_{\text{bio}})^{b_m} \right], \quad (9)$$

where  $G_a$  is cumulative probability of mortality (0–1),  $t_{\text{bio}}$  is cumulative developmental status for adults, and  $b_m$  is an empirical, best-fit parameter (Table 1).

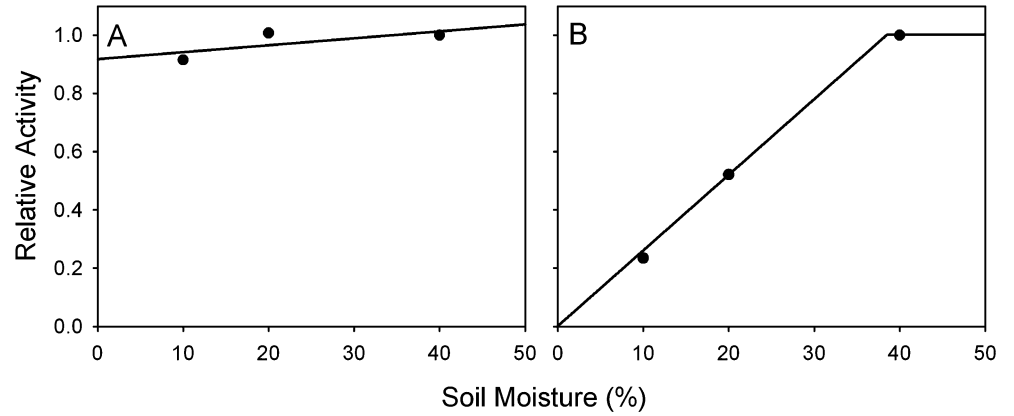
#### Soil moisture effect

We simulate the response of Collembola to soil moisture ( $E$ ) as a scalar multiplier for calculated rates of survival (Eq. 2) and reproduction (Eq. 5) based on observations from laboratory experiments using an artificial soil (Choi et al. 2002):

$$E_l = c_l + d_l H, \quad (10)$$

where  $l$  is relative activity (s indicates survival and r, reproduction),  $H$  is soil moisture (percentage by weight),

**Fig. 1** Effects of soil moisture on survival (a) and reproduction (b) of *Paronychirus kimi*



and  $c_1$  and  $d_1$  are best-fit parameters (Table 1 and Fig. 1). This relationship assumes maximum survival and reproduction at a soil moisture value of 40%, which corresponds to 152% of field capacity (26%) for soils from the field site, because survival and reproduction were constant when soil moisture was at least 40% (Kang et al. 2001).

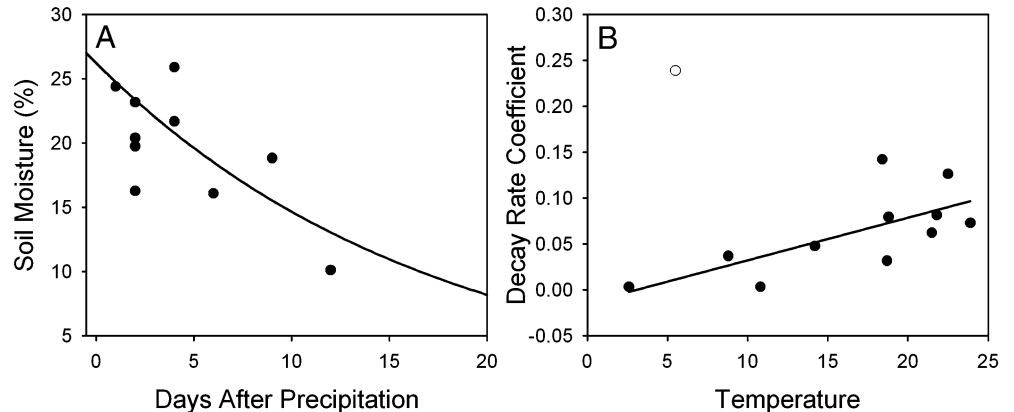
#### Paraquat application

We estimate effects of a spring herbicide application (paraquat; *N,N'*-dimethyl- $\gamma$ , $\gamma'$ -bipyridylium dichloride) on survival and reproduction of *P. kimi* based on results of laboratory experiments (Choi 2001). At the recommended application rate (500 ppm), survival and reproduction fell by 5 and 31%, respectively, over a period of 4 weeks:

$$\begin{aligned} D_{i,a} &= (1-0.05)D_{i,b} \\ N_a &= (1-0.31)N_b, \end{aligned} \quad (11)$$

where  $a$  and  $b$  are after and before application of herbicide, respectively,  $i$  is the life stage,  $N$  is the number of eggs, and  $D$  is density of Collembola. Paraquat was applied on May 1 in our model, with effects that lasted for 28 days.

**Fig. 2** Relationship between soil moisture and days following precipitation (a) and best-fit estimate of decay rate coefficient for water loss vs temperature (b). Open circle indicates datum excluded from analysis



#### Soil moisture and temperature regimes

We obtained daily precipitation, ambient, and soil temperature values from the South Korean Meteorological Administration. We found that soil temperature ( $T_s$ ) could be approximated as a sine function of time based on observed values from the field site ( $n=365$ ,  $r^2=0.97$ ):

$$T_s = q + u \sin(2\pi L/365 + s), \quad (12)$$

where  $L$  is Julian day, and  $q$ ,  $u$ , and  $s$  are best-fit parameters (Table 1).

Soil water flux is the net difference between precipitation inputs and losses due to drainage and evapotranspiration. Precipitation infiltrates the surface soil (depth 10 cm) until it exceeds field capacity (approximately 26% by weight), and excess precipitation is lost through drainage. Water loss from soil through evapotranspiration is a negative exponential function of time since rainfall, with the decay rate coefficient defined as a linear function of temperature:

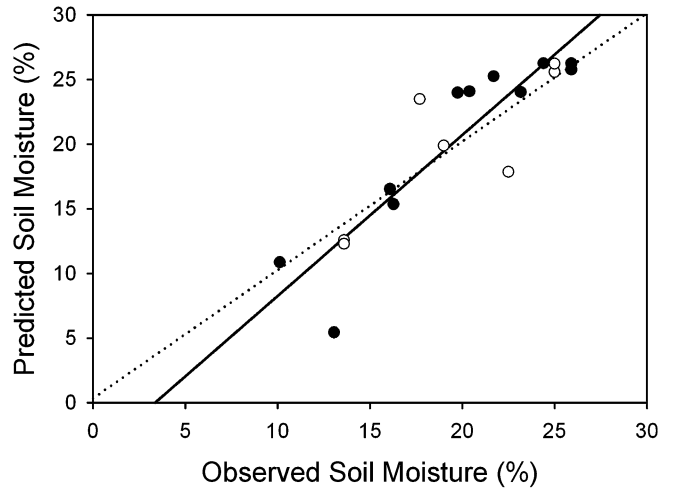
$$H_t = H_0 \exp[-(m + n T) t], \quad (13)$$

where  $H_t$  is soil moisture at time  $t$  (days after precipitation),  $T$  is ambient temperature, and  $m$  and  $n$  are best-fit parameters (Table 1). These estimates of the relationships between the coefficient of decay and ambient temperature

(Fig. 2b;  $n=11$ ,  $r^2=0.48$ ), and soil moisture loss over time (Fig. 2a;  $n=11$ ,  $r^2=0.35$ ) capture much of the dynamics of soil moisture for the study site (Fig. 3;  $r^2=0.83$  and  $0.70$  in 1998 and 1999, respectively, Fig. 4).

**Results**

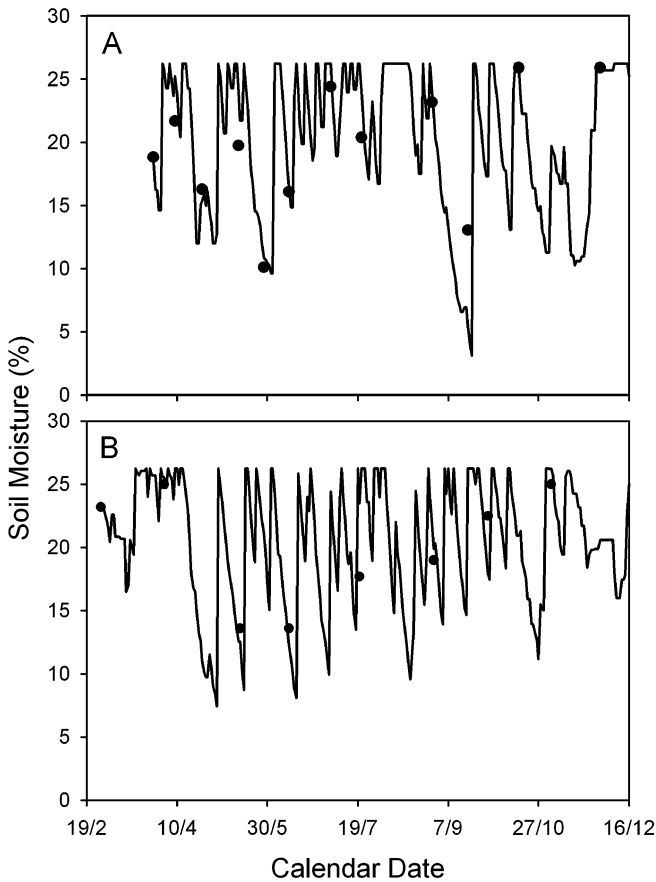
The population model produced a stable limit cycle within 2 years of simulation when driven by the sine curve of approximate soil temperatures (Fig. 5a) but omitting the effects of soil moisture. The overall pattern of results suggested the persistence of low numbers of adults and declining numbers of juveniles through winter, and four rapid flushes of egg production during spring and summer, which in turn drove dampening flushes of juvenile and adult cohorts. The last flush of juveniles appeared in late autumn and apparently fueled an increase in adult population in early spring of the subsequent year (Fig. 5b). The simulated density of juvenile and adult collembolans approximated the observed pattern of field populations (Fig. 6a). Removing one outlier produced a significant correlation between simulations and observations ( $n=12$ ,  $r^2=0.40$ ,  $P<0.05$ ; Fig. 6b) but not when the outlier was included ( $n=13$ ,  $r^2=0.18$ ,  $P>0.05$ ). In either case, differ-



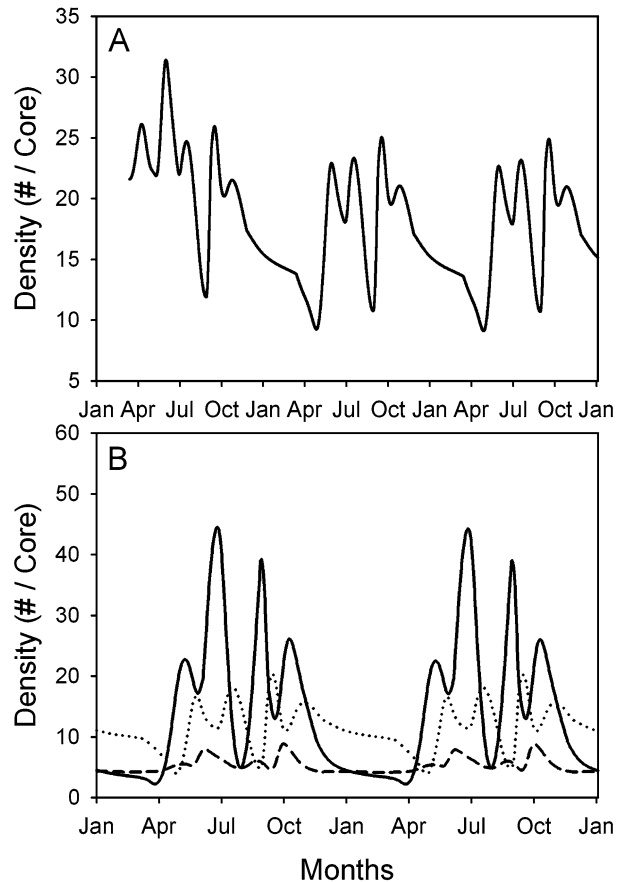
**Fig. 4** Relationship between simulated and observed soil moisture:  $r^2=0.83$  and  $0.70$  in 1998 (dotted line and closed circles) and 1999 (solid line and open circles), respectively

ences between observations and simulations increased throughout the year.

Including the effects of soil moisture on survival and reproduction reduced the overall population levels during the year, bringing our estimates into closer correspondence

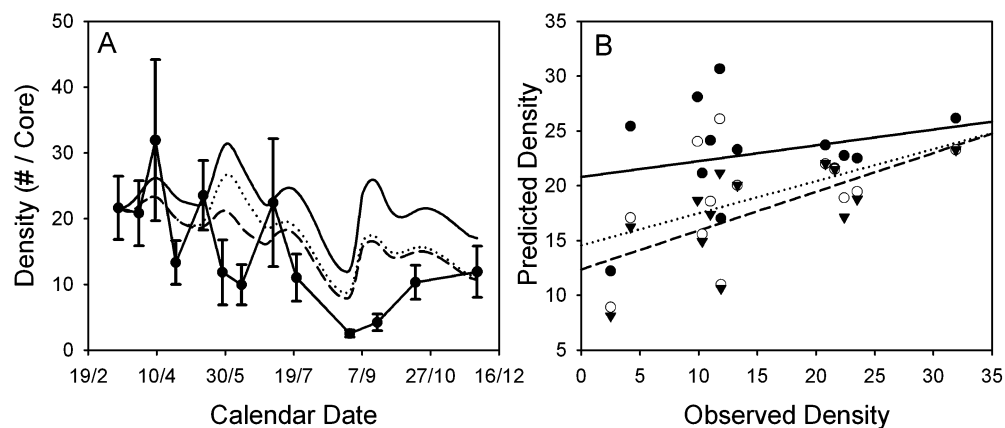


**Fig. 3** Estimated and observed percent gravimetric soil moisture at the field site in 1998 (a) and 1999 (b). Circles and the solid line indicate observed values and simulated values predicted by the regression model, respectively



**Fig. 5** Total population (juveniles + adults) dynamics simulated by the model without including soil moisture effects (a) and changes in density of each stage for years 2 and 3 (b): solid line, eggs; dotted line, juveniles; and dashed line, adults

**Fig. 6** Seasonal changes in population density of *Paronychiurus kimi* in 1998 (a) and linear correlation of simulated and observed population density in 1998 (b). Observed density (mean±SE) in the field (solid line with filled circles and error bars) and results of models using temperature driver exclusively (solid line and filled circles), temperature and moisture drivers (dotted line and open circles), and temperature, moisture, and herbicide drivers (dashed line and triangles) are illustrated



with observations (Fig. 6a) and increasing the coefficient of determination ( $r^2$ ) from 0.18 to 0.40 (Fig. 6b). In particular, moisture limitations tended to decrease populations in the middle and later portions of the year when initial differences between simulations and observations were greatest.

Adding the effects of paraquat further increased the correspondence between simulated and observed densities (Fig. 6a), and increased the coefficient of determination ( $r^2$ ) to 0.45 (Fig. 6b). When mortality and reproduction were affected by paraquat application in early May, the predicted population density of *P. kimi* declined from May to June during a period in which differences between simulations and observations were otherwise inexplicably high.

## Discussion

Soil invertebrates live in an environment of fluctuating temperature and moisture conditions. Although indicators of soil community activity such as respiration and mineralization rates are influenced by both factors, few population models of soil invertebrates have explicitly included the effects of moisture. Earlier field and laboratory studies suggested that moisture conditions likely affect field population dynamics of *P. kimi*, a common soil-dwelling Collembola in South Korea (Choi et al. 2002; Choi and Ryoo 2003). Results of our modeling study confirm this notion.

The dynamics of our model without including soil moisture effects produce a stable limit cycle within 2 years of simulation (Fig. 5a), suggesting overall stability of the model given a temperature regime generally representative of field conditions and physiological characteristics based on previous laboratory studies of this species. Oscillations in populations of eggs, juveniles, and adults are driven by low rates of fecundity, development, and mortality in winter, followed by flushes of cohorts passing through development at increasing rates as temperatures increased through summer, and slowing with declining temperatures during autumn (Fig. 5b). Comparisons between simulated and observed densities indicate a significant, albeit variable, relationship (Fig. 6a). Simulated populations roughly follow temporal patterns of field densities but show fewer extreme fluctua-

tions and tend to increasingly overestimate populations as the summer progresses (Fig. 6a).

Many authors suggest that Collembola prefer high humidity (Sjursen and Holmstrup 2004), and they report greater population density with precipitation and with irrigation (Ferguson and Joly 2002). Our simple soil moisture model estimates field conditions that compare well with observations (Fig. 4), although observations are inadequate to validate much of the simulated dynamics of soil moisture (Fig. 3). Adding the modest effects of soil moisture on survival and substantial effects on fecundity of *P. kimi* (Fig. 1) improves the correspondence between simulated and observed population levels (Fig. 6a). In particular, moisture limitations decrease population levels as the summer progresses and soils become drier (Fig. 6a). However, simulations are still less variable than observations and still tend to overestimate field densities of *P. kimi*. Comparisons between years in our study suggest that moisture conditions in 1998 were less favorable for population development of *P. kimi* than in 1999, and possibly an important limiting factor for population dynamics. Thus, results of our model simulations are consistent with those suggesting that soil moisture and precipitation are major limiting factors to soil Collembola.

The precise mechanisms underlying the effects of moisture on collembolan population dynamics are unclear, but collembolan locomotion apparently declines as an immediate response to dry conditions (Testerink 1982). For example, Bauer and Christian (1993) report that another temperate species, *Onychiurus armatus* (Tullberg), remains immobile during severe moisture stress, even until death. These observations suggest that lower moisture availability can reduce reproductive activity as an indirect effect of lower individual movement, reducing sexual interactions between individuals rather than exerting a direct physiological effect on reproduction. This may explain why moisture affects fecundity more than survival of *P. kimi* and *F. candida*, another common, temperate collembolan species (van Gestel and van Diepen 1997). In any case, our model demonstrates a significant impact of reduced fecundity with moisture stress that improves correspondence between simulated and observed population densities (Fig. 1).

Aside from climatic effects, field populations of *P. kimi* show an unpredictable decline in May and June, at a time when increasing temperatures and reasonably moist conditions increase simulated densities. Neither temperature nor moisture limitations alone can explain this observed decline, nor can our model produce this pattern from cohort dynamics or lags in population dynamics. This discrepancy between simulations and observations corresponds to the timing of an herbicide application, paraquat, on the study site (embankments of a rice field). Including the effects of paraquat application into the model partly explained this discrepancy. Other studies also report a reduction in density of soil microarthropods with xenobiotic applications primarily through lowered reproduction (Al-Assiuty and Khalil 1996; Kang et al. 2001). Collembola such as *Isotoma anglicana* Lubbock, *Heteromurus nitidus* (Templeton), *Lepidocyrtus violaceus* (Fourcroy), *F. candida*, and *O. armatus* appear to avoid Betanal, a common herbicide (Heupel 2002). This avoidance behavior requires energy perhaps otherwise allocated to survival and reproduction, and may thus reduce population growth. In addition, herbicides may change soil microclimate by reducing vegetation in ways that are unfavorable to Collembola, perhaps by increasing surface evaporation. Højer et al. (2001) show that drought can induce higher mortality of *F. candida* under exposure of 4-nonylphenol than at optimum soil humidity. Regardless of precise mechanism, including an inhibitory effect of paraquat on collembolan populations helps to explain discrepancies between simulated and observed population dynamics and suggests a real, negative impact on field populations.

Our model is among the first to demonstrate significant impacts of soil moisture and herbicide application on field population dynamics of a common soil-dwelling collembolan species. Thus, this model has potential for use not only in assessing the impacts of changes in soil temperature, moisture, and xenobiotics regimes for soil microarthropods but also in understanding their contribution to both decomposition and mineralization processes in soil through estimating production, respiration, and egestion rates coupled with biomass. Moreover, knowledge of such combined impacts on the population dynamics of key groups of organisms provides a basis for a more mechanistic understanding of community response and concomitant insight to ecological processes related to soil fertility.

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