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Life-history trade-offs of *Paronychiurus kimi* (Lee) (Collembola: Onychiuridae) populations exposed to paraquat

Won Il Choi[a,*], Deborah A. Neher[a], Mun Il Ryoo[b]

[a]Department of Plant and Soil Science, University of Vermont, 105 Carrigan Drive, Burlington, Vermont 05405, USA
[b]Division of Environmental Science and Ecological Engineering, College of Life and Environmental Sciences, Korea University, Anam-Dong, Sungbuk-Gu, Seoul 136-701, Republic of Korea

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Abstract

The demography of *Paronychiurus kimi*, a dominant collembolan in paddy fields of Korea, was quantified for four treatments of the herbicide paraquat (0, 1.6, 16, 160 and 1600 μg/cm^2) in a controlled environment using plaster-of-Paris as the test substrate. The survival rate of adults and the reproductive fitness of *P. kimi* were not affected by paraquat except at the highest dosage (1600 μg/cm^2), when fed baker's yeast and reared on plaster–charcoal substrate. However, results of life-history experiments suggest that fitness was maintained by a tradeoff between fecundity and reproductive period. It is suggested that these are potential life-history tradeoffs of Collembola that were exposed to the manufacturer's recommended concentration of paraquat (16 μg/cm^2).

Keywords: Collembola; Demographical bioassay; Fitness; Herbicide; Life history; Paraquat

1. Introduction

Herbicides are one of the major xenobiotics applied to agricultural soil and its use has increased because of high costs of labor. Paraquat is a dominant herbicide used in Korean rice paddy fields (Lee et al., 2001) and its impact on ecosystems is controversial (Bromilow, 2003). Collembolans are useful organisms to assess the ecological risk of paraquat on soil ecosystems because they are important as fragmenters of organic matter and consumers of microbes (Crossley et al., 1992; Fountain and Hopkin, 2005; Seastedt, 1984).

Demographical bioassays conducted as life-history experiments are useful tools because they detect changes of life-history traits throughout the life span of organisms including both survival and reproduction parameters. Because fitness is determined by multiple life-history traits, analysis of tradeoffs among these traits may offer insight into the parameters of fitness that are sensitive to exposure of xenobiotics. For example, Kammenga et al. (1997) showed that fitness of a nematode, *Plectus acuminatus*, can be compensated by a tradeoff between survival and fertility when it is exposed to a moderate concentration of pentachlorophenol. They determined that daily fertility was insensitive to exposure to pentachlorophenol because it was constant rather than variable during the experimental period. In contrast, daily or weekly fertility of collembolans is age dependent and, thus, affects fitness of Collembola when exposed to xenobiotics (Choi et al., 2002). Therefore, modifications of Kammenga's model are necessary if applied to Collembola.

The present study was conducted to evaluate the influence of the herbicide, paraquat, on the demography of *P. kimi* (Lee), a dominant springtail of the paddy fields in Korea (Kang et al., 2001). Because herbicides are applied to the paddy fields in spring when temperatures are suitable to reproduction of *P. kimi* (Choi and Ryoo, 2003; Choi et al., 2002), paraquat has the potential to affect reproduction of this species. The objective of this study was to assess the effect of paraquat on the survival

*Corresponding author. Current address: Division of Forest Disease and Insect Pests, Korea Forest Research Institute, 207 Cheongyangni-2 dong, Dongdaemun-gu, Seoul 130-712, Republic of Korea.
Fax: +82 2 961 2679.
E-mail addresses: wchoi@foa.go.kr, choi_71@hanmail.net (W.I. Choi).

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and reproduction of *P. kimi* and to analyze these data from the perspective of life-history tables (Kammenga et al., 1997).

2. Materials and methods

2.1. Collembola

P. kimi was collected from a rice field in Ichon, located in the central region of Korea, in September 1996. These *P. kimi* were maintained on baker's yeast (*Saccharomyces cerevisiae*) in glass crystal dishes (height 90 mm, diameter 90 mm) on a base of plaster-of-Paris mixed with charcoal in the ratio 4:1. The relative humidity in the glass dish was maintained at 100% by spraying weekly with distilled water.

2.2. Chemical

Paraquat (1, 1′-dimethyl-4, 4′, -bipyridinium dichloride) is one of the most frequently used herbicides worldwide due to its non-selectivity against annual and perennial plant species (Bromilow, 2003). Target plants are unable to metabolize it completely, thus leaving residues adsorbed to soils and sediments (Eisler, 1990). In the present study, a commercial formulation containing 24.5% active ingredient of paraquat (Hankook Samgong Co. Ltd.) was used.

2.3. Demography of P. kimi exposed to paraquat

The experimental unit was a Petri dish (90 mm diameter, 15 mm height) containing 20 six-week-old adult collembolans on a solid base of plaster–charcoal–distilled water in 3:1:3 by volume. Appropriate amounts (50, 500, 5000 or 50,000 μg/mL) of paraquat in 2 mL distilled water were sprayed onto the populated substrate using a Potter spray tower at 0.70 kgf/cm^2 (Burkard Manufacturing, Rickmansworth, England). Treated experimental units were incubated at 20 °C under continuous darkness. The final dosages corresponded to 0, 1.6, 16, 160, and 1600 μg/cm^2 based on the surface area of each dish, respectively. The collembolans in the dish treated with 2 mL of distilled water served as a control. Each treatment was replicated three times. The animals were not fed during the first week of treatment. Adult mortality and eggs laid were recorded every week and the surviving adult springtails were transferred to a fresh Petri dish filled with the substrate provided with 10 mg yeast without further treatment of paraquat. Life history of the animal was observed until reproduction of all springtails ceased.

2.4. Estimation of life table statistics

Based on the data on the age specific survival rate and fecundity, the intrinsic rate of natural increase (r_m) per week was estimated using Lotka's equation (see Pielou, 1969):

$$\int_0^{\infty} e^{-r_m} lxmx\,\mathrm{d}x \approx \sum_0^{\infty} e^{-rm} lxmx = 1, \tag{1}$$

where l_x is the age specific survival rate per week, m_x the age specific fecundity per week, x the midpoint age (week) of the female, and r_m the intrinsic rate of natural increase. The intrinsic rate of natural increase (r_m) was estimated using the maximum likelihood method. The generation time (GT) (week), finite rate of increase (λ) (week^{-1}), and net reproduction per generation (R_0) was estimated from the equations (see Pielou, 1969):

$$\mathrm{GT} \approx \sum xlxmx \Big/ \sum lxmx, \tag{2}$$

$$l = \exp(r_m), \tag{3}$$

$$R_0 = \sum lxmx. \tag{4}$$

2.5. Life-history tradeoff and sensitivity analysis

To simulate the sequential changes in the survival rate $S(x)$, the survival data were fitted to a Weibull function defined as (Pinder et al., 1978)

$$S(x) = 1 - \left(1 - \exp(-(x/b)^c)\right), \tag{5}$$

where x is age, and b and c are parameters of the function (Table 1). A formula based on $S(x)$ is used to fit the cumulative reproduction, $R(x)$, which is defined as

$$R(x) = a\left(1 - \exp(-(x/b)^c)\right), \tag{6}$$

where a, b and c are parameters. The parameters a, b and c of Weibull function represent constant for cumulative reproduction, the shape and scale of the function, respectively. Therefore, in case of fecundity function, b would reflect reproductive pattern (Pinder et al., 1978).

The age specific survival rate (l_x) and fecundity (m_x) were estimated by Eqs. (5) and (6), respectively. Estimates of survival rate and fecundity were incorporated into Eq. (1) and this equation was used to estimate reproductive fitness of collembolan populations at each concentration of paraquat. In addition, the equation was also used for sensitivity analysis to assess effects of the total number of eggs laid and CRT_{50} on fitness. A sensitivity analysis was performed using Matlab version 6.1 software (Natick, MA, USA).

3. Results

Survival rates of *P. kimi* adults were similar for paraquat dosages ranging from 0 to 160 μg/cm^2, but were reduced significantly at 1600 μg/cm^2 (Fig. 1a) (based on 95% CI). The number of eggs produced over 20 weeks of *P. kimi* adults unexposed to paraquat (i.e., controls) was 33.76 per female. Cumulative reproduction values were greatest (i.e., 43.77 per female) when collembolans were exposed to paraquat at 1.6 μg/cm^2 and decreased with increasing dosage (Fig. 1b). Except for the highest dosage in our experiment, the linear relationship between b and c can be estimated to be

$$c = 3.91 - 0.30\,b\,(r^2 = 0.88), \tag{7}$$

Table 1
Parameters (±SE) of the Weibull function for survival and cumulative reproduction of *Paronychiurus kimi* under influence of paraquat treatment on charcoal-plaster at 20 °C and 95–100% relative humidity (Fig. 1). Parameters b and c are constants for the shape and scale of the function. Parameter of a is a measure for fertility of cumulative reproduction and is considered as 1 for survival curve

Dosage (μg/cm^2)	a	se	b	se	c	se
Survival						
0	—	—	14.85	0.30	1.35	0.06
1.6	—	—	13.90	0.25	0.70	0.02
16	—	—	18.44	0.44	1.13	0.06
160	—	—	15.13	0.38	0.99	0.05
1600	—	—	5.61	0.25	0.60	0.03
Reproduction						
0	33.76	0.30	8.22	0.13	1.61	0.06
1.6	43.77	0.45	7.28	0.15	1.63	0.08
16	23.87	0.23	6.60	0.13	1.82	0.09
160	17.03	0.13	5.09	0.09	2.50	0.16
1600	17.36	0.17	8.17	0.12	2.50	0.13

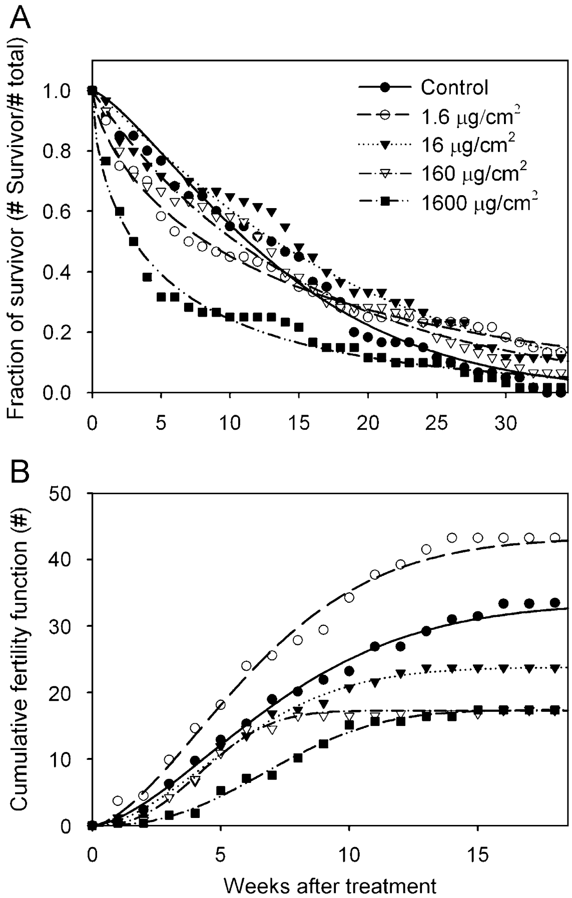

Fig. 1. Survival (A) and cumulative reproduction (B) of adult *Paronychiurus kimi* exposed with four different dosages of paraquat on charcoal–plaster substrate at 20 °C. The survival rate and the cumulative reproduction were estimated by Eqs. (5) and (6), respectively. Dots and lines indicated observed and estimated values, respectively. See Table 1 for the estimated Weibull parameters.

where b and c are parameters of the Weibull function estimated empirically for each experimental treatment (Table 1, Fig. 2a). To estimate the reproductive period of collembolans, the half cumulative reproductive time (week) (CRT_{50}) is defined as the time of half the total reproduction and is calculated by solving Eq. (6) follows:

$$0.5 = a\left(1 - \exp\left(-(x/b)^{(3.91-0.30\,b)}\right)\right), \tag{8}$$

where a and b are constants of the Weibull function estimated empirically for each experimental treatment (Table 1, Fig. 2b). Because the shape of the function is independent on parameter a of the Weibull function (personal observation), CRT_{50} values that corresponded to b values ranged from 5.1 to 8.3 with a iterative step interval of 0.1 estimated by solving Eq. (8). The derived values were used to estimate relationship between parameter b of the Weibull function and the half cumulative reproductive time (CRT_{50}) (Fig. 2b):

$$CRT_{50} = 1.16 + 0.64\,b\,(r^2 = 0.99). \tag{9}$$

Likewise, CRT_{50} values (half of cumulative reproductive time) were 6.55 weeks for unexposed collembolans and decreased with increased dosages of paraquat up to 160 μg/cm^2 (Fig. 3). In contrast, CRT_{50} values increased to 7.06 weeks at 1600 μg/cm^2 of paraquat. This suggests that *P. kimi* exposed to paraquat produced eggs for a shorter period of time than unexposed collembolans, with the exception of extremely high dosages of paraquat that delay reproduction.

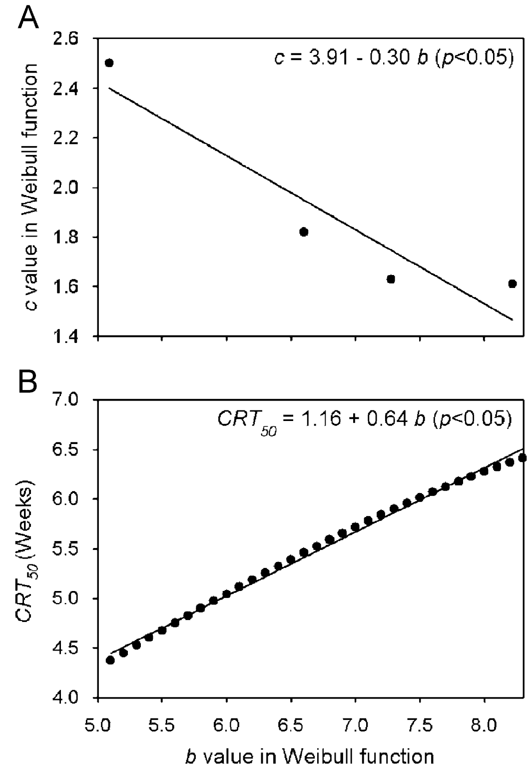

Fig. 2. Relationship between b and c value in Weibull function presented in Eq. (5) (A), and between CRT_{50} and b value in Weibull function according to Eq. (9) (B). Circles and the solid line indicate observed values and simulated values predicted by the regression model, respectively. All of values in the figures were estimated from the paraquat toxicity experiment to *Paronychiurus kimi* on the charcoal–plaster (Fig. 1).

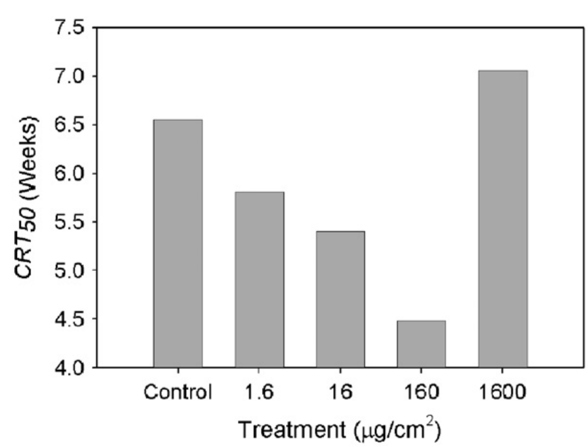

Fig. 3. Effects of paraquat dosage (μg/cm^2) and the 50th percentile of half cumulative reproductive time (CRT_{50} expressed in weeks) of *Paronychiurus kimi* on charcoal–plaster.

The intrinsic rate of natural increase (i.e., fitness) (r_m) was 0.24/week for unexposed *P. kimi* populations whereas it was greater (i.e., 0.27/week) for collembolans exposed to paraquat at 1.6 $\mu g/cm^2$. At dosages greater than 1.6 $\mu g/cm^2$, r_m values decreased with increasing dosages of paraquat (Table 2). Similar trends were observed for net reproductive rate (R_0, Table 2). The fitness of *P. kimi* exposed to 16 $\mu g/cm^2$ decreased 4.2% compared to control, whereas R_0 of *P. kimi* exposed to 16 $\mu g/cm^2$ decreased 24.3%.

Values of b ranged from 5.0 to 8.0, which coincided with our experimental range were affected negatively by values of c and positively by values of CRT_{50} (Fig. 4). Fig. 4 shows the results of the sensitivity analysis of fitness under influence of CRT_{50} (represented by b value) and number of eggs laid/female and the relationship was described as

$$r_m = 0.25 - 0.0092\,b + 0.0029\,\text{egg}\,(r^2 = 0.99), \quad (10)$$

where r_m is fitness, and *egg* is the number of eggs laid during the experimental period. This equation suggests that fitness of Collembola increased with increasing number of eggs laid with constant CRT_{50} value and decreased with increasing CRT_{50} with constant fertility. Thus, a collembolan population would increase in fitness without a simultaneous increase in fertility by concentrating its reproduction in earlier reproductive period. This phenomenon was inferred by smaller CRT_{50} values. In our experiment, the fitness of Collembola exposed to paraquat at 16 $\mu g/cm^2$ showed a similar life-history tradeoff. However, the tradeoff was unable to fully compensate reduced fertility by decreased CRT_{50} values (i.e., earlier reproduction during the reproductive period).

Table 2
The life table statistics of *Paronychiurus kimi* maintained on charcoal–plaster treated with paraquat at 20 °C and 95–100% relative humidity

Dosage ($\mu g/cm^2$)	r_m	GT	λ	R_0	DT
0	0.24	14.26	1.28	22.67	2.84
1.6	0.27	13.42	1.31	25.62	2.55
16	0.23	13.48	1.26	17.15	3.05
160	0.20	12.40	1.23	11.50	3.38
1600	0.12	14.80	1.13	5.32	5.87

r_m: intrinsic rate of natural increase per week, GT: generation time (week), λ: finite rate of increase per week, R_0: net reproduction rate per generation, DT: doubling time (week).

4. Discussion

Collembola can compensate for decreased fertility under exposure to paraquat by concentrating egg production early in their reproductive period. Although other scientists have studied effects of herbicides on Collembola (AlAssiuty and Khalil, 1996; Amorim et al., 2005; Ponge et al., 2002; Rebecchi et al., 2000; Sabatini et al., 1998; Sarkar et al., 2000; Siepel, 1995), to the best of our knowledge, this is among the first studies to show life-history traits tradeoff of Collembola exposed to an herbicide. Exposure to

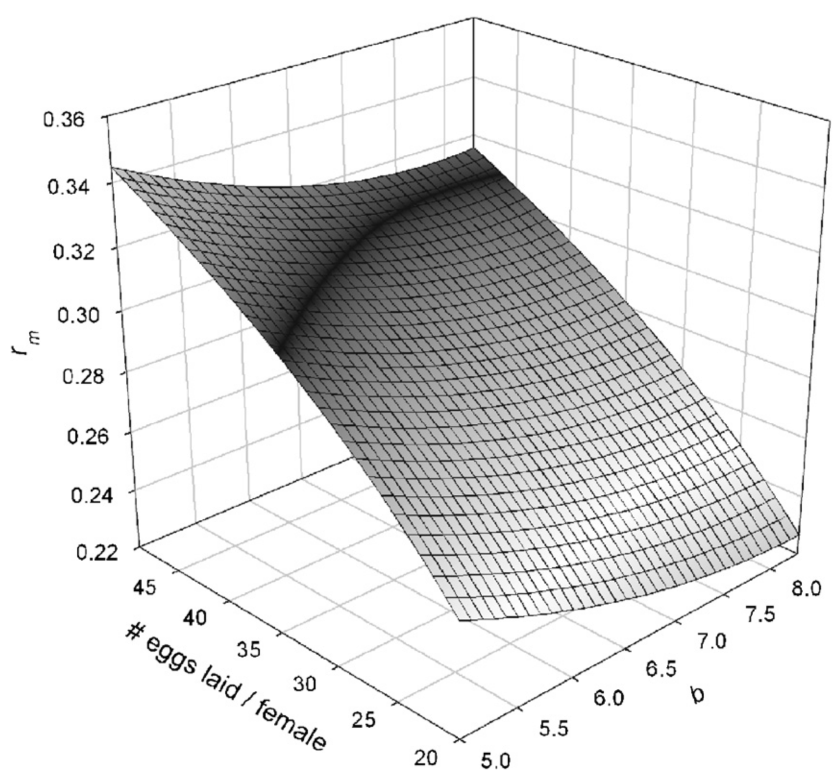

Fig. 4. Results of sensitivity analysis using Eq. (1). The analysis shows the influence of b value and the number of eggs laid/female on r_m. Here, b is a parameter of Weibull function given in Eq. (5).

paraquat induced two changes in life-history trait of *P. kimi*: decreases in fecundity and concentrating reproduction earlier in the reproductive period. These two traits are components of fitness and results of our sensitivity analysis suggest that reduced fertility and delayed reproduction cause decreased fitness. Consequently, *P. kimi* concentrates its reproduction earlier in adulthood, achieving greater fitness than those populations that distribute their reproduction evenly throughout adulthood. We demonstrated that *P. kimi* exposed to paraquat compensates its fitness using phenotypic plasticity. Evidently, the net reproduction rate decreased 24.3% at the recommended dose (16 μg/cm^2) compared to unexposed collembolans, and fitness decreased only 4.2%. This suggests that other life-history traits compensate for lower fertility of *P. kimi* when exposed to dosages of paraquat of 16 μg/cm^2 or greater. Therefore, *P. kimi* exposed to paraquat at recommended doses show life-history traits tradeoff to maintain its' fitness. This conclusion is supported by Kammenga et al. (1997) who demonstrates that phenotypic plasticity in life-history traits, such as juvenile survival and daily reproduction, can compensate the fitness of *P. acuminatus*, a nematode exposed to moderate concentrations of pentachlorophenol.

Interestingly, *P. kimi* exposed to a relatively low dosage of paraquat (1.6 μg/cm^2) appeared to have greater fitness, exhibiting both greater fecundity and concentrating its reproduction during an earlier reproductive period. Certainly, there is a possibility that our dose did not coincide with field dosage due to difference in bioavailability between experimental media such as plaster/charcoal, artificial soil, and field soil (Kang et al., 2001; Lock and Janssen, 2001a, b). Nonetheless, our results showed that paraquat has the potential to stimulate reproduction of *P. kimi* at low concentrations. A similar phenomenon was reported in the nematode, *Acrobeloides* sp. exposed to copper (Li et al., 2005). The phenomenon is referred to as hormesis, the stimulated biological response often seen at low concentration of chemicals (Calabrese, 2005). The mechanism of this phenomenon is unclear but some authors suggest that xenobiotics may stimulate metabolism of organisms exposed to low doses of xenobiotic chemicals.

Recently, Lopes et al. (2004) reported that *Daphnia* exposed to copper solution had greater fertility and tolerance to copper than those from an uncontaminated site. Perhaps this phenomenon can be explained by loss of very sensitive individuals due to lower fitness or by fixing phenotypic plasticity induced by life-history traits tradeoff genetically during the adaptation process. However, it is uncertain whether paraquat may induce changes in genetic or phenotypic composition of collembolan populations and, in turn, affect their tolerance to the herbicide because paraquat is persistent in soil but its bioavailability is limited because of strong binding to clay particles. Although some authors suggest that residual concentration of paraquat in Korean agricultural fields is relatively high (Lee et al., 2001), bioavailability of the herbicide to Collembola is unknown. Therefore, comparative experiments with Collembola exposed to herbicide-contaminated and herbicide-free sites are necessary to clarify the effects of paraquat on microarthropod populations.

To date, the influence of paraquat treatment on soil ecosystems is controversial (Bromilow, 2003, Choi et al., 2006). Edwards (1970) observed that paraquat had no apparent effect on micro-invertebrates at recommended dosage. His results suggest that paraquat may not directly cause mortality of the collembolans. Likewise, Riley and Wilkinson (1976) noted that earthworms were not affected directly by paraquat at a recommended dose applied to soils at different stages of cultivation. Subagja and Snider (1981) reported similar results that paraquat did not cause acute mortality of *Tullbergia granulata* and *Folsomia candida* on polluted food at concentrations ranging from 600 to 5000 μg/g in controlled environments. In contrast, reproduction of collembolans decreased when they were offered food contaminated by paraquat at a concentration of 600 μg/g. Curry (1970) observed a reduction of Collembola in grasslands after it had been sprayed with paraquat at the recommended manufacturer's dose and, thus, suggested that indirect effects such as removal of plants are a possible cause for decrease of springtail community.

In conclusion, our results suggest that an application of paraquat has a potential to affect population dynamics of *P. kimi* even without apparent reduction in survival and reproduction of the microarthropod. In addition, our results show that collembolan fitness can be maintained by life-history traits tradeoff under herbicide stress. This suggests that physiological or biochemical responses may enable adaptation of collembolans to a stressful environment. Therefore, low concentrations of xenobiotics can induce biochemical or molecular reactions that correspond with life-history tradeoffs.

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