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The effects of drought upon epigeal Collembola from arable soils

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Abstract

1 Springtails (Hexapoda, Collembola) are usually associated with moist microhabitats. However, some species show adaptations to ecosystems subjected to periodic desiccation. This study examined the effects of short-term drought conditions upon epigeal Collembola collected from arable fields.
2 An emergence trap was used in the laboratory to investigate collembolan activity, particularly the emergence of newly hatched juveniles from soils subjected to a simulated drought and to varied levels of simulated rainfall.
3 Addition of water to soils subjected to a 4-month simulated drought resulted in synchronized emergence of juveniles of *Sminthurinus elegans*, *Sminthurus viridis* and *Bourletiella hortensis*. As anhydrobiotic nymphs were not found in the soil, these juveniles are likely to have recently hatched from eggs in the soil.
4 The same species were shown to emerge when desiccated soil samples were treated with simulated heavy rainfall. No emergence occurred in soils which received no water, whilst only a few juveniles were present under a regime of the lowest monthly rainfall recorded for the area in the spring.
5 This study provides the first evidence that in northern European arable systems some epigeal Collembola can survive considerable periods of drought as eggs, emergence of which is triggered by rainfall. These findings have implications for the effects of predicted climatic changes upon collembolan populations, the recovery of collembolan communities following pesticide applications in agroecosystems, and also provide a plausible mechanism for dispersal of Collembola as wind-blown eggs.

Keywords Aestivation, anhydrobiosis, climate change, desiccation, dispersal, pesticide side-effects, springtails, temperate agroecosystems.

Introduction

The incidence of droughts has increased over recent years in temperate areas such as the U.K. where the climate has been predicted to get warmer and drier, and appears to be doing so (e.g. Markham, 1996). These changes in climate, generally attributed to global warming, are predicted to produce changes in the British flora and fauna and are therefore the subject of numerous studies (e.g. Cummins *et al*., 1995; Masters *et al*., 1998). Effects are most likely to influence organisms which are known to be sensitive to humidity changes. Epigeal springtails (Hexapoda: Collembola) may be influenced by the occurrence of drought, because they are prone to desiccation as most species lack true tracheal systems and breathe through their integument. Humidity and temperature are known to be critical factors in their distribution (Joosse & Groen, 1970; Verhoef, 1981; Verhoef & Van Selm, 1983).

Certain species of Collembola have become adapted to periodically dry environments. Work carried out in Australian deserts and in dry Mediterranean ecosystems has shown that some Collembola have several strategies for coping with dry conditions (Greenslade & Greenslade, 1973; Greenslade, 1982). These are: morphological and physiological adaptations to tolerate high temperatures and low humidities; inactive, desiccated drought-resistant adult or juvenile stages which can be reactivated by moisture, known as anhydrobiosis and ecomorphosis; and desiccation-resistant eggs, which can hatch when humidity increases (see Greenslade, 1981, for a general review). These adaptations were found in members of both symphypleonid and arthropleonid Collembola.

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Previous work has suggested that several species of Symphypleona are better adapted to an epigeal lifestyle than most arthropleonids, by having morphological adaptations such as a primitive tracheal system and thicker integument. These have enabled them to colonize soil surfaces which are more variable and drier than the soil itself (Betsch & Vannier, 1977; Betsch *et al*., 1980; Eisenbeis & Wichards, 1987). The avoidance of summer drought by aestivation has been detected in *Sminthurus viridis* (Linnaeus) (Maclagan, 1932) and in certain other species (e.g. *Onychiurus meridiatus,* Argyropoulou & Stamou, 1993). *Folsomides angularis* and *Brachystomella parvula* were reported to survive through dry mediterranean summers in an anhydrobiotic state (Poinsot, 1968, 1974).

The potential effects of drought on the majority of the Collembola species of temperate agroecosystems remain unknown. In arable fields, Collembola are extremely widespread and play an important role in decomposition and in maintaining soil structure (Naeem *et al*., 1995; Vreeken-Buijs & Brussard, 1996). They are also an alternative food source for beneficial predators of importance for Integrated Pest Management (IPM) (Sunderland *et al*., 1997). Long-term studies have suggested that the use of some pesticides produces strong detrimental effects upon collembolan populations (Vickerman, 1992; Filser, 1995; Frampton, 1997). Aestivation as eggs, or anhydrobiotic adults or juveniles, has implications both for the exposure and recovery of Collembola subject to pesticide use in arable fields. This could lead to reduced exposure to pesticides and, if eggs and adults have different susceptibilities to pesticides (Chernova *et al*., 1995), changes in the overall susceptibility of field populations.

Our aim in this study was to determine whether epigeal Collembola from arable soils aestivate during periods of drought in the U.K., and to identify the species which could survive drought conditions. We developed an emergence trap to infer the presence of collembolan eggs or anhydrobiotic stages in soils by detecting their activity before and after water was made available. The developmental stage of the individuals caught immediately after watering the soil was used to differentiate between anhydrobiotic adults as opposed to desiccation-resistant eggs; the dried soils were investigated prior to watering and found to contain no anhydrobiotic juveniles. The early immature stages could therefore be assumed to have hatched recently. This technique was then used to determine the range of species of Collembola which aestivated in soil taken from arable fields.

Materials and methods

Design of emergence traps

Emergence traps were designed to be used in the laboratory to trap live, surface-active arthropods from field-collected soils. The traps comprised plastic trays (each 1500 cm^3) half-filled with soil (900 g), which were kept in the laboratory at room temperature (20–25°C). Two pitfall traps (Petri dishes, 3.5 cm diameter) were placed in the trays such that their rims were level with the soil surface, and filled with water. A drop of liquid detergent was added to the water in the traps to reduce surface tension. Trays were covered with cotton cloth of mesh size 200–250 µm and kept in a room with closed windows to prevent colonization from external sources. The contents of the pitfall traps were collected weekly, and were examined under a binocular microscope for the organisms present.

The efficiency of the pitfall traps was tested by releasing a known number of wild-caught Collembola into each of four replicate emergence traps. The species released were *Sminthurus viridis, Sminthurinus elegans* (Fitch)*, Isotoma viridis* Bourlet*, Deuterosminthurus* spp. and the *Lepidocyrtus* species *cyaneus* Tullberg and *violaceus* Tullberg. Because Collembola can reproduce in the soil trays, the percentage recapture rate was calculated using the total catch after one week to ensure that the catch only included the original Collembola released.

Egg survival in the laboratory

To investigate the presence of Collembola in fields in the early spring prior to crop sowing, 10 trays of surface soil (the top 20 cm) were taken from six randomly chosen locations in the centres of two fields ('Scrapps' and 'Danny') in the Manydown Company Estate, Wooton St Lawrence, Hampshire (56° 16′ N 1° 10′ W). The two fields were chosen as they had similar cropping and pesticide application histories, but slightly different soil types (calcareous flinty and silty clay loam). Samples were collected on 16 March 1996 then each was passed through a 3.5 × 20 mm rectangular coarse sieve to ensure a uniform mixing of the top soil layer, and 900 g from each sample were placed in a tray as described above. The trays were randomly allocated to positions on a work bench and were incubated under controlled laboratory conditions (20–25°C; L:D 12 : 12 h) for 2 months. The soil was kept moist by watering with a hand-held mister every 2 days or as required to maintain the soil saturated. Contents of the pitfall traps were recorded weekly. The soils were then allowed to dry out for 4 months in the laboratory to represent a worst case scenario by simulating a long summer drought. The dryness of the soil was verified by calculating its moisture content which was less than 5% (water content levels of 20% are considered as relatively dry in field experiments, see Amellal *et al*., 1998). The soil moisture content was calculated by heating the sample to 105°C for 24 h so that all the moisture evaporated, after which no further change in weight occurred. The traps were reset for one week and found to contain no Collembola, after which soils were watered again on the surface to simulate rainfall. The Collembola catch was then recorded at weekly intervals for 4 weeks. Repeated measures ANOVA with field as a fixed variable was carried out in order to compare the catches over time from the soils from the two separate fields. Repeated measures ANOVA was also carried out to compare the mean numbers of Symphypleona and Arthropleona trapped over time.

Effects of different simulated rainfall treatments

Samples were collected on 24 April 1997 from a field located on the Leckford Estate, Hampshire (51° 8′ N 1° 29′ W). This area had been exposed to early spring drought conditions as there had been considerably less than average rainfall for 2 months. The total rainfall for March 1997 at the site was 29.1 mm, less than half of the 1961–96 average (64 mm; data for Hampshire available from the Meteorological Office). The top 15–25 cm of soil (calcareous flinty clay loam) were collected from random positions in a recently ploughed strip alongside a field of winter wheat, at least 6 m from the nearest hedge. The soil was sieved in the laboratory and divided between 15 plastic trays, as described above. Samples of soil were sorted under a binocular microscope to find out whether adults or nymphs were present in the soil as anhydrobiotic forms.

The trays were then randomly allotted to a treatment. Three simulated rainfall treatments were used: no water (control: simulated drought); 1.9 mm per week (minimum realistic rainfall); and 23.7 mm per week (maximum realistic rainfall). These figures were calculated from the 1961–96 data on rainfall in Hampshire from March–May (Meteorological Office data). Water was applied for between 1 and 4 min in each tray twice a week, using a hand-held mister and sprayed uniformly over the soil surface. To prevent the complete flooding of the trays, excess water was allowed to drain out through a small hole in the base of the tray. These treatments were continued for 6 weeks, during which pitfall contents were examined twice a week for 6 weeks. In order to verify whether any differences among catches of emerging Collembola were due only to the different water treatments, after 6 weeks all the soils were watered with the average rainfall equivalents (12.5 mm per week) and the catches were recorded twice a week for a further 2 weeks.

Taxonomic identification

Species were identified using a binocular microscope; specimens difficult to identify were mounted and examined using a compound light microscope. Identification was carried out with the aid of Christiansen & Bellinger (1998), Fjellberg (1980) and Stach (1947, 1956, 1963). *Lepidocyrtus cyaneus* and *L. violaceus* were grouped together as they appear to be similar in their response and are referred to in the text as *Lepidocyrtus* spp.

Table 1 Recapture rates one week after Collembola were released into the emergence traps in order to test their efficiency (four replicates).

Species	Mean percentage recapture (SE; number released)
Lepidocyrtus spp.	54.6 (12.2; $n = 62$)
Smithurus viridis	57.2 (12.7; $n = 35$)
Isotoma viridis	62.7 (13.6;$n = 130$)
Sminthurinus elegans	90.9 (3.5; $n = 117$)
Deuterosminthurus spp.	42.1 (20.5; $n = 74$)

Results

Efficiency of the emergence traps

The recapture rates of five species of Collembola in the emergence traps are shown in Table 1. The recapture rate varied between 42.1% (SE 20.5%) for *Deuterosminthurus* spp., to 90.1% (SE 3.5%) for *S. elegans.* Hence these traps were useful for trapping diverse species of mobile epigeal Collembola in a controlled laboratory situation.

Survival of eggs following a 4-month simulated drought

Captures previous to the period of simulated drought showed that Arthropleona, comprising *I. viridis, I. palustris* and *Lepidocyrtus* spp. were present as adults in the 1996 spring-collected soil. Subsequent captures of juveniles were probably due to reproduction in the soil trays (Table 2). Initial captures of Symphypleona, namely *S. elegans, Bourletiella hortensis* Fitch and *S. viridis* were predominantly of juveniles. This suggests that these species had been present as eggs or anhydrobiotic immatures in the soil samples (Table 2). No significant differences in capture numbers were found between the soils from the two fields for most of the species hatched (*S. elegans* $F_{1,7} = 0.12$, $P > 0.05$; *S. viridis* $F_{1,5} = 1.16$, $P > 0.05$; all Symphypleona $F_{1,7} = 0.68$, $P > 0.05$; all Arthropleona $F_{1,7} = 0.96$, $P > 0.05$; zero values among the counts of *I. viridis*, *I. palustris* and *Lepidocyrtus* spp. precluded statistically supported comparisons), suggesting that these two fields contained a similar epigeic collembolan fauna, except for *B. hortensis* ($F_{1,7} = 8.03$, $P < 0.05$). The very high numbers of *S. elegans* trapped over time suggest that this species may have been breeding successfully in the soil trays.

Following the 4-month period of simulated drought, the soil trays were watered again. Figure 1a shows that despite having been present in the soils immediately after collection, no Arthropleona (*I. palustris, Lepidocyrtus* spp. or *I. viridis*) were caught after the drought. Only Symphypleona were captured after the drought, the majority being *S. elegans.* The catches of

Table 2 Species found in or emerging from soil collected in the early spring from two arable fields in Hampshire. Soils were incubated under laboratory conditions. The total catch numbers from both soils is shown consisting of adults (A) and juveniles (J).

Time incubated (weeks)	*B. hortensis*	*S. elegans*	*S. viridis*	*I. viridis*	*I. palustris*	*Lepidocyrtus* spp.
1	1A	5J	44J	25J & A	4A	50A
2	6J & A	19J	54J	14J & A	2A	10A
3	8J & A	4J	4J	1J	0	5A
4	10J & A	10J & A	11J	2J	0	1A
5	64J & A	52J & A	26J	1J	0	8J & A
6	0	224J & A	2J	1J	0	0
7	6J & A	260J & A	0	13J	0	6J
8	1J	355J & A	0	59J	2J	4J

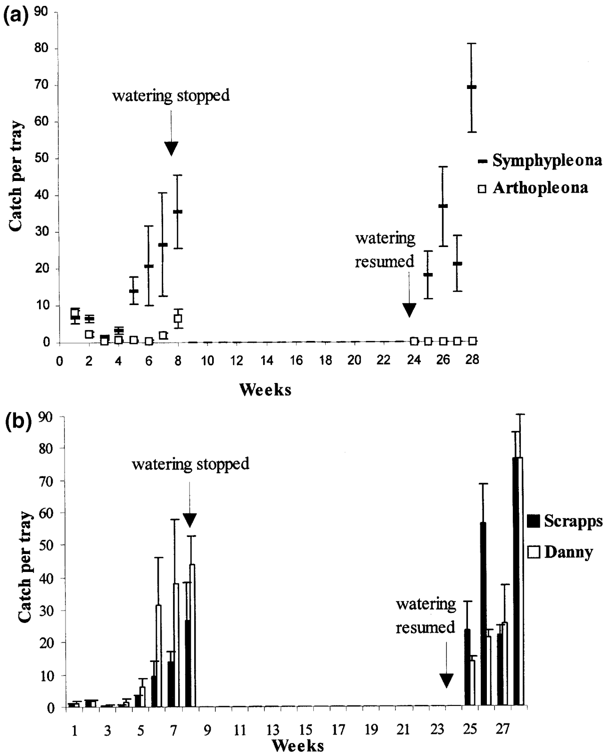

Figure 1 Emergence patterns of Collembola from soils collected in the spring of 1996 from two fields ('Scrapps' and 'Danny'). Soils which were kept humid for the first 8 weeks were allowed to dry out to simulate a 4-month summer drought, after which watering was resumed. (a) Differences in hatching between Arthropleona and Symphypleona (mean number from both soils + SE). (b) The emergence pattern of *S. elegans* (mean number from both soils + SE).

these two groups differed significantly overall ($F_{1,16} = 141.8$, $P < 0.001$), with symphypleonids being more numerous. *Sminthurinus elegans* was trapped before and after the drought period (Fig. 1b); only juveniles were caught in the first samples postwatering. Other species of Symphypleona for which juveniles were captured included *B. hortensis* and *S. viridis*; other juveniles which were captured could not be identified accurately but comprised less than 5% of the catch.

Species emerging under different rainfall simulation treatments

The dry soils collected from a field exposed to early spring drought which were subjected to different watering regimes produced very clear results in the first 6 weeks. Only the soils that were watered had surface-active Collembola present, and the highest catch occurred under the maximum rainfall treatment (Figs 2a and b) in all but two occasions, when a higher catch was recorded under the minimum rainfall treatment (Fig. 2b). Only Symphypleona were captured. The most common species caught was *S. elegans* (Fig. 2a) and significant differences were found between the treatments, with the greatest catch occurring under the maximum rainfall treatment ($F_{2,12} = 72.8$, $P < 0.001$). Samples from the first week were composed wholly of juveniles, whereas later samples comprised a mixture of adults and juveniles. No anhydrobiotic juveniles were found in the dry soil samples prior to watering, so the juveniles which emerged can be assumed to have hatched from eggs. Desiccated adults of *Lepidocyrtus* spp. were found, but these are unlikely to have been viable as none were caught in the traps detecting surface activity. Other Collembola emerged as juveniles but could not be identified accurately and none was captured as adult. They are included here as 'all other Collembola' (Fig. 2b) and again significant differences were found in the catch means between the three rainfall treatments ($F_{2,12} = 21.4$, $P < 0.001$).

The soils from all three levels of simulation rainfall treatments were subsequently supplied with the manipulated equivalent of average rainfall. Juveniles of *S. elegans* and other symphypleonids subsequently emerged from the soils in all the trays (Figs 2a and b), suggesting that the trigger for emergence was water availability, as all other abiotic conditions were kept constant. Significant differences between the catch means from the different treatments were still found after this watering occasion (*S. elegans* $F_{2,12} = 6.5$, $P < 0.05$; other Symphypleona $F_{2,12} = 3.9$, $P < 0.05$). The lower number of individuals emerging from the maximum-rainfall trays at this stage is likely to have been due to a depletion in the desiccation-resistant population present in the soil, as emergence had been occurring in these trays from the beginning of the experiment.

Discussion

These experiments gave an insight into the capacity of arable field Collembola to withstand drought. Whilst a 4-month period of drought in the U.K. has only occurred on extremely rare occasions in the south of England, it is not uncommon at lower latitudes. We used a 4-month early to late spring drought to represent a worst case scenario for the Collembola in British arable fields.

Species of Collembola adapted to periodic drought have been found in Australian and Mediterranean ecosystems (e.g. Poinsot, 1968, 1971, 1974; Greenslade & Greenslade, 1973; Vannier, 1973; Greenslade, 1981, 1985), as well as in the Antarctic where desiccation occurs due to the extreme cold (Holmstrupp & Sömme, 1998). Some of these desiccation-resistant species are encountered in temperate European arable fields, in particular *Lepidocyrtus* spp. (Wood, 1971), *Pseudosinella* spp. (Greenslade, 1981), *Isotomurus palustris* Müller (Poinsot, 1971), *I. viridis* (Poinsot, 1971), *I. notabilis* (Poinsot, 1971), *Sminthurus aureus* Lubbock (Poinsot, 1971) and *S. viridis* (Betsch-Pinot, 1980). Our study found evidence for the existence of desiccation-resistant stages only in *S. viridis* amongst this list of Collembola. Other species which have previously been found aestivating did not hatch out under our experimental set-up, despite being common in the fields from which the samples were taken (e.g. *Lepidocyrtus* spp., *I. palustris*, *I. viridis*, *I. notabilis*; Alvarez *et al.*, 1997). Previous studies in Europe have found that the populations of some Collembola were not detrimentally affected by dry periods (e.g. *Entomobrya nivallis* (L.) – Verhoef & Van Selm, 1983, and *Orchesella cincta* (L.) – Verhoef & Li, 1983).This is the first time that drought resistance of collembolan eggs has been demonstrated in temperate climates such as the U.K. Other species, which had not been previously reported to have drought resistant eggs, were *S. elegans* and *B. hortensis*.

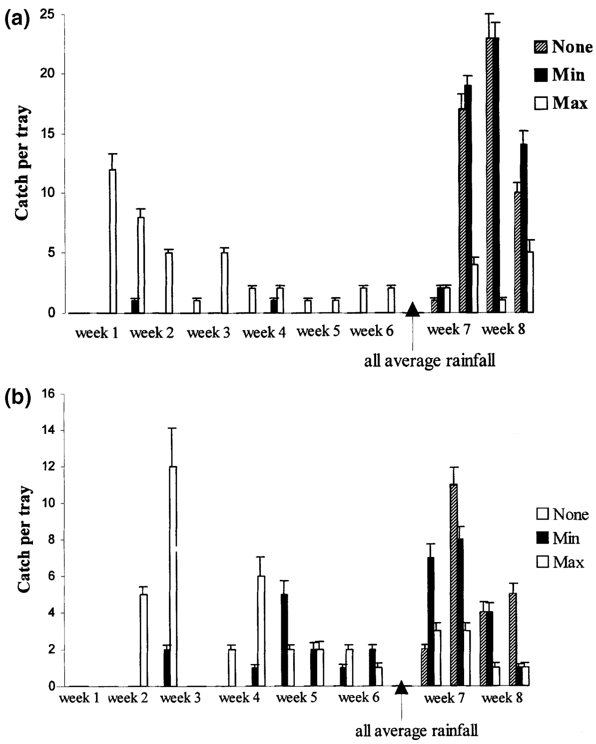

Figure 2 Emergence of Collembola from soils exposed to three simulation rainfall treatments during weeks 1–6. 'None' received no water; 'Min' received minimum rainfall equivalent to 1.9 mm per week; 'Max' received maximum rainfall equivalent to 23.7 mm per week. From week 7 all trays received the water volume equivalent to average rainfall. (a) Total number of adult and juvenile *S. elegans* caught in the emergence traps (mean number + SE). (b) Total Collembola trapped excluding *S. elegans* (mean number + SE).

Our results suggest that some of the symphypleonid Collembola of European arable fields have desiccation-resistant egg stages; no emergence occurred of arthropleonid species, which could be due to a lack of a resistant egg, or juvenile, stage. However, this requires further testing, as under this experimental set-up other factors may have affected the presence of arthropleonid eggs: these could include physical damage caused by the sieving of the soils, abiotic conditions in the laboratory and the different phenologies of species so that egg stages were simply not present at the time samples were collected. Future studies should investigate soils taken at different times of the year. As our samples were taken in the early spring the eggs present may have been overwintering or freshly laid, but they are clearly also capable of surviving drought. In a recent review, Block (1996) suggested that drought tolerance mechanisms in arthropods could also pre-adapt them for tolerating freezing and *vice-versa*, as both factors involve desiccation. Hence, overwintering populations of Collembola in the field could be less susceptible to drought than summer or autumn populations, a possibility which requires further investigation. Further studies investigating the viability of drought-stressed eggs in relation to a variable egg moisture content could also help to elucidate the responses by different species to dry conditions.

The ability of some Collembola to survive through periods of desiccation has several implications. Desiccation tolerance may affect the capacities for passive aerial dispersal of these species. Dormant eggs could also be important sources of population recovery following the use of pesticides, and could alter the community composition available for monitoring pesticide or pollution effects. There will also be implications for the effects of climatic change upon the northern European arable field fauna.

This study has shown that an inexpensive, simple emergence trap can be used successfully in the laboratory to study the emergence of surface-active Collembola from diverse soils. We have shown that *S. elegans* is able to survive desiccation for up to 4 months in a dry soil, apparently as eggs. This is the first time that this survival trait has been shown to occur in this species in the U.K. It is also the first time that this drought-resistant adaptation has been demonstrated in collembolan species which do not habitually live in arid environments, i.e. which are not strictly xerophilic. This has important implications for the ecology of Collembola in arable ecosystems and suggests that alterations in collembolan community composition may be a useful monitoring tool for detecting effects of climatic change. Further studies are required to identify how long dormant eggs can persist in different soil types, what other factors trigger hatching, and whether these eggs can survive aerial dispersal.

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