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ORIGINAL ARTICLE

Water relations and drought sensitivity of *Folsomia candida* eggs (Collembola: Isotomidae)

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Abstract. Drought tolerance of juvenile and adult life stages is relatively well understood, but very little is known about the tolerance of eggs to drought in this group of animals. The aim of the present study was therefore to investigate the water relations and drought sensitivity of eggs of the hygrophilic springtail, *Folsomia candida* Willem, 1902 (Isotomidae), exposed to a range of soil water potentials above and below the permanent wilting point of plants (–1.5 MPa). Under saturated conditions, eggs absorbed water during development and increased water content from 1.1 to 2.9 mg mg^{-1} dry weight. By increasing drought conditions, water absorption was gradually reduced and was nullified approximately at the soil water potential equivalent to the osmolality of egg fluids (630 mOsm corresponding to –1.53 MPa). Eggs had a lower permeability for water (68 ± 13 µg water cm^{-2} h^{-1} mm Hg^{-1}) than adults (about 400 µg water cm^{-2} h^{-1} mm Hg^{-1}), but eggs were much more sensitive to drought than adults. Eggs did not survive exposure to –1.5 MPa, whereas adults readily survive this level of drought by absorbing water vapour. In conclusion, eggs of *F. candida* are sensitive to drought and would perish if soil water potential in the field approaches the wilting point of plants, which is often reached during summer droughts. The persistence of this species depends on the survival of post-embryonic life stages.

INTRODUCTION

Springtails (Collembola) are geographically widespread soil arthropods that can occur at high densities approaching 10^5 individuals m^{-2} or more (Petersen & Luxton, 1982). Although springtails are relatively small (often below 5 mm in body length), they play significant roles in terrestrial ecosystems by influencing decomposition and nutrient recycling processes in the soil (Bardgett, 2005). Since springtails and many other soil invertebrates need high soil moisture contents for optimal functioning, even small decreases in soil water potential can have negative effects on their growth, reproduction and survival (Wallwork, 1970; Vannier, 1987; Hopkin, 1997; Holmstrup, 2001; Waagner et al., 2011). Recent syntheses and predictions of climate change suggest that summer droughts are increasing in frequency and intensity (IPCC, 2013), making an understanding of the effects of these climatic extremes ever more important (Siepel, 1996; Blankinship et al., 2011).

Adult and juvenile life stages of soil living springtails are not very resistant to desiccation compared to, e.g., insects (i.e. they are unable to reduce evaporative water loss) since their skin is permeable to water vapour (Harrison et al., 1991; Kærsgaard et al., 2004). Despite their permeable skin, many species can tolerate drought conditions far below the wilting point of plants (soil water potential of –1.5 MPa) by absorbing water vapour made possible by the accumulation of compatible osmolytes such as myo-inositol, trehalose and alanine (Bayley & Holmstrup, 1999; Sjursen et al., 2001; Holmstrup et al., 2015). Some species can tolerate severe water loss or even enter anhydrobiosis and survive drought for long periods (Poinsot, 1968; Poinsot-Balaguer & Barra, 1991; Holmstrup, 2018). In addition to these physiological defence mechanisms, juvenile and adult springtails can migrate to moister soil layers or microsites and thus improve their chances of survival during drought by behavioral means (Hågvar, 1983; Verhoef & Van Selm, 1983; Detsis, 2000; Tsiafouli et al., 2005).

Springtail eggs are, of course, confined to the habitat in which they are produced. Many springtails lay eggs in the superficial soil layers, which are most prone to desiccation during drought. Moreover, many species of springtails begin egg-laying in the field during late spring and early summer when droughts can be frequent (Hale, 1965; Joosse, 1969). This suggests that springtail eggs are often exposed to drought conditions that potentially can delay embryonic development or even cause egg mortality (Thibaud, 1968; Alvarez et al., 1999). Despite the importance of the susceptibility of eggs to drought for the population dynamics and ecology of springtails, very few experimental studies have addressed this problem. Moreover, the few studies that exist have tested relative humidities (RH) below 95% (Choudhuri, 1963; Thibaud, 1968)

whereas the soil drought conditions that occur in nature are most often associated with RHs above 98% (Hillel, 1998). As pointed out by Vannier (1987) drought stress is best quantified by measuring the soil water potential because this allows for a mechanistic understanding of the water balance and osmotic relationships of organisms in relation to their environment.

The soil living species, *Folsomia candida* Willem, was chosen as a suitable model for the present investigation. This species is common in temperate forest and open land soils, and has been widely used as test organism in a range of ecophysiological, ecotoxicological and ecological studies (Fountain & Hopkin, 2005). *Folsomia candida* reproduces by apomictic parthenogenesis and has an egg-to-egg life cycle of about 25 days at 20°C. In laboratory cultures the species produces egg clutches (30–150 eggs per clutch). Moulting occurs every 4–5 days and the adults may live and reproduce (after every second moult) for more than 200 days (Snider, 1973). The aim of this study was to investigate the water relations and drought susceptibility of *F. candida* eggs exposed to the soil water potentials recorded in natural drought conditions. This investigation included measurement of the water content of eggs during development, rates of water loss, duration of embryonic development and egg mortality under a range of soil water potentials above and below the permanent wilting point of plants (–1.5 MPa).

MATERIAL AND METHODS

Experimental animals and egg production

Folsomia candida was cultured in Petri dishes the base of which contained a moistened gypsum/charcoal mixture (8 : 1 w : w). The springtails were kept at a constant 20°C (12L : 12D) and given dried baker's yeast as feed. For synchronized egg production, adult springtails were transferred to newly produced Petri dishes, which stimulated egg laying (Krogh, 1995). After one day, adults were removed and the egg clutches collected for the experiments. Duration of egg development for the clone used in the present experiment was 10–12 days at 20°C (M. Holmstrup, unpubl.), which is similar to other reports (Marshall & Kevan, 1962; Stam et al., 1996).

Water content and size of eggs during development at optimal humidity

Egg clutches (0–24 h of age) deposited on moist gypsum/charcoal (i.e. saturated humidity conditions) were incubated at 20 ± 0.1°C (12L : 12D). After different periods (6–192 h), the diameter of about 20 randomly selected eggs was determined using an eyepiece micrometer at 100× magnification (to the nearest 0.01 mm). Further, egg clutches (containing 150–300 eggs) were transferred to pre-weighed tin caps. Gravimetric water content was determined by weighing samples before and after oven drying at 60°C for 24 h. Weighings were done using an electron balance with a precision of 0.001 mg (Micro SC 2, Sartorius AG, Goettingen, Germany).

Osmolality of egg contents

The osmolality of the contents of eggs was determined by vapour pressure osmometry using Wescor C-52 sample chambers connected to a Wescor HR 33T Dew Point Microvoltmeter operated in the dew point mode (Wescor Inc., Logan, Utah). Combined egg clutches (ca. 1.5 mg fresh weight or about 1,200 eggs) were transferred to a sample holder of the C-52 chambers and crushed using a cylindrical aluminium rod that fitted into the sample holder cavity. The accuracy of this equipment is within ± 10 mOsm.

Drought tolerance

Survival (i.e. hatchability of eggs) was determined after a 7-day exposure to a range of water potentials. Clusters of newly produced eggs were placed in pre-weighed tin caps (3 × 9 mm) using a fine paint brush. The fresh weight of egg clusters was determined to the nearest 0.001 mg (Micro SC 2, Sartorius AG, Goettingen, Germany) and the number of eggs was estimated based on the average egg fresh weight (Table 1). The tin cap was placed in a small plastic vial (3 cm high, 1.6 cm diameter). The vials were covered with a 100 µm nylon mesh and each vial was then placed in the centre of a 160-ml plastic beaker (4.2 cm high, 7 cm diameter) containing an aqueous NaCl solution. Aqueous NaCl solutions (from 2 to 32 g L^{-1}) were used to establish eight levels of increasing drought from –0.11 (control) to –2.48 MPa (Table 2). The beakers were kept in a polystyrene box to minimize temperature fluctuations and the experiment was conducted in a climate room at a constant temperature of 20 ± 0.1°C. After exposure to drought, the tin caps with eggs were transferred to moist gypsum-charcoal in 5.5 cm diameter Petri dishes and kept at 20°C. The eggs were inspected daily for another 14 days until all surviving eggs had hatched. The time until the first hatch was noted and the number of juveniles that emerged was counted for each of six replicates. Egg survival was calculated as the number of juveniles divided by the estimated number of eggs exposed.

Water content after exposure to drought

The water content of eggs was determined at the end of a 7-day exposure to the same drought conditions as described in the section above ("Drought tolerance"). Again, clusters of newly produced eggs were placed in pre-weighed tin caps (3 × 9 mm) using a fine paint brush. The initial fresh weight of egg clusters (FW_{init}) was determined to the nearest 0.001 mg, and the eggs were exposed to drought as described. At the end of the exposure to drought, the tin caps with eggs were weighed again (giving the fresh weight of the eggs exposed to drought; $FW_{drought}$). After drying for 24 h at 60°C, dry weight (DW) was determined. Initial

Table 1. Fresh weight, water content, diameter, osmolality and permeability of newly produced eggs of *Folsomia candida*.

Parameter	Mean ± S.D.
Fresh weight (µg egg^{-1})	1.31 ± 0.07 (*N* = 4)*
Water content (mg mg^{-1} dry weight)	1.12 ± 0.04 (*N* = 6)
Egg diameter (mm)	0.131 ± 0.005 (*N* = 18)
Osmolality (mOsm kg^{-1})	631 ± 79 (*N* = 5)
Permeability (µg water cm^{-2} h^{-1} mm Hg^{-1})	68 ± 13 (*N* = 6)

* Four batches of 160–300 eggs were weighed and counted.

Table 2. Concentration of NaCl in aqueous solutions with corresponding relative humidity (RH) of the air in equilibrium with these solutions and the corresponding soil water potential (Weast, 1989).

g NaCl L^{-1}	RH (%)	Water potential (MPa)
2	99.9	–0.11
4.1	99.8	–0.27
8	99.5	–0.59
12	99.3	–0.91
16.1	99.1	–1.24
24	98.7	–1.88
28	98.4	–2.17
32	98.2	–2.48

water content (WC_{init}) and water content at the end of the exposre to drought ($WC_{drought}$) was calculated as mg water mg^{-1} DW. The relative water gain during the 7-day drought exposure was calculated as $[(WC_{init} - WC_{drought}) / WC_{init}] \times 100\%$. DW was assumed to remain constant during the experiment.

Rate of water loss and permeability

The rate of water loss was determined for groups of eggs by repeated weighing at room temperature and humidity. In brief, groups of eggs (between 48 and 112 eggs) were spread out on pre-weighed pieces of aluminium foil (measuring 10 × 10 mm). During 48 min, the decrease in fresh weight of each group of eggs was followed at six-minute intervals. The eggs were placed next to the microbalance and the temperature and air RH close to the eggs were logged using a Tinytag Plus 2 (model TGP-4500) humidity and temperature datalogger with a precision of 0.1% RH and 0.1°C (Gemini Data Loggers Ltd, Chichester, UK). The temperature and humidity was virtually constant at 24.1°C and 35.0% RH. The rate of water loss of six groups of eggs was determined. The permeability was calculated as µg water lost cm^{-2} surface h^{-1} $unit^{-1}$ saturation deficit (mm Hg). The saturation deficit was 14.625 mm Hg at 35.0% RH and 24.1°C (Weast, 1989). The surface and volume of single eggs was calculated using the approximation that they were roughly spherical and had an average diameter of 0.13 mm (Table 1). Although this estimate of surface area and permeability is not perfect, it is sufficient for comparisons with other arthropod eggs and adult *F. candida*.

Statistical analysis

Data were subjected to one-way ANOVA and post hoc pairwise comparisons were done using the Holm-Sidak method. Analyses were done using Sigmaplot for Windows Version 12.0 (Systat software Inc., Chicago, IL, USA).

RESULTS AND DISCUSSION

This study is the first of its kind to describe permeability, water relations and survival of springtail eggs in well-controlled drought experiments. This study therefore adds to our knowledge of the responses of springtails to drought conditions in the soil (although only one temperature was used), and improves the possibilities for predicting how springtail populations in nature may respond to climatic changes.

Water uptake by insect eggs during embryonic development is well-known (Hadley, 1994). Embryonic development has been studied in a number of species of springtails including *F. candida* (Tieg, 1942; Marshall & Kevan, 1962), however, no studies have attempted to quantify the water content as done here. *F. candida* eggs had an initial water content of 1.12 mg mg^{-1} DW (Table 1), which increased significantly during the experimental period of 8 days (one-way ANOVA; F = 144.3; $P < 0.001$; Fig. 1A). Water content had almost tripled (2.9 mg mg^{-1} DW) by the end of the experiment and there was a close correspondence between water content and egg volume (Fig. 1B). The osmolality of newly produced eggs was about 630 mOsm (Table 1), which is somewhat higher than the haemolymph osmolality of juvenile and adult *F. candida*, which is 300–400 mOsm (Bayley & Holmstrup, 1999; Holmstrup et al., 2015). The relatively high osmolality of eggs accounts for the uptake of water, likely by passive absorption, during development in Petri dishes where moisture was close to saturation. Water content apparently reached a plateau when the embryonic development approached completion at the end of the experiment (Fig. 1A).

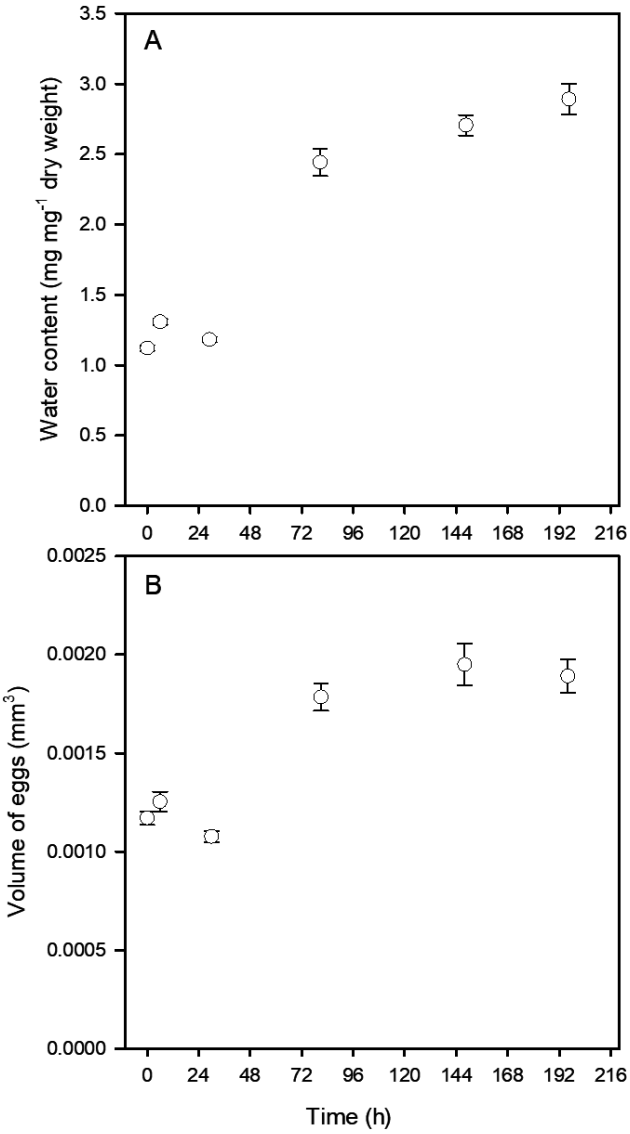

Fig. 1. Water content (A) and egg volume (B) of *Folsomia candida* eggs during the first 8 days of embryonic development at 20°C. The values are means ± SE (water content: *N* = 6; volume: *N* = 18–20).

The estimated permeability of eggs was 68 ± 13 µg water cm^{-2} h^{-1} mm Hg^{-1} (Table 1), which is similar to the permeability of eggs of insects from moist environments, but much higher than insects from dry habitats (Edney, 1977). Interestingly, the permeability of eggs was much lower than the permeability of juvenile and adult *F. candida,* which is estimated to be ca. 400 µg water cm^{-2} h^{-1} mm Hg^{-1} (Kærsgaard et al., 2004). The low permeability of eggs is probably a result of evolutionary processes since eggs are small, with a large surface:volume ratio, which increases the rate of water loss under drought conditions, and they cannot actively seek out more favourable micro-habitats like the mobile life stages (Hadley, 1994). Eggs of *F. candida* are laid in clusters consisting of up to several hundred eggs (Snider, 1973; Stam et al., 1996), which is bound to

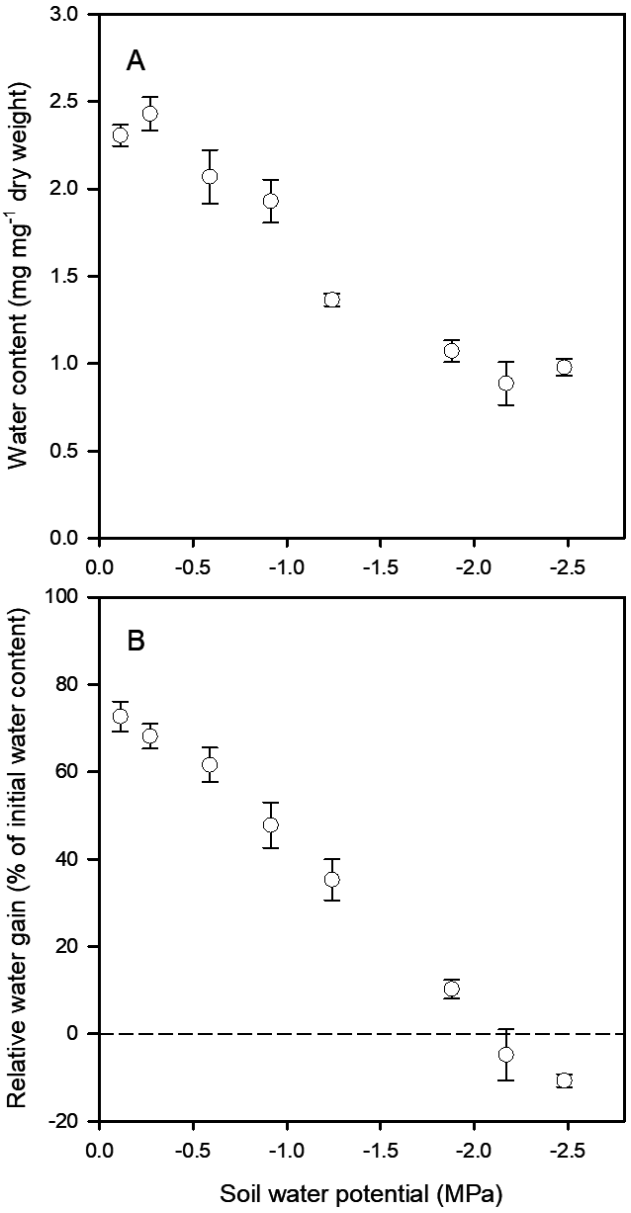

Fig. 2. Absolute water content (A) and relative water gain during development (B) of *Folsomia candida* eggs at the end of a 7-day exposure to varying levels of drought. The values are means ± SE (*N* = 6). The dashed line in (B) indicate no net water gain relative to initial water content.

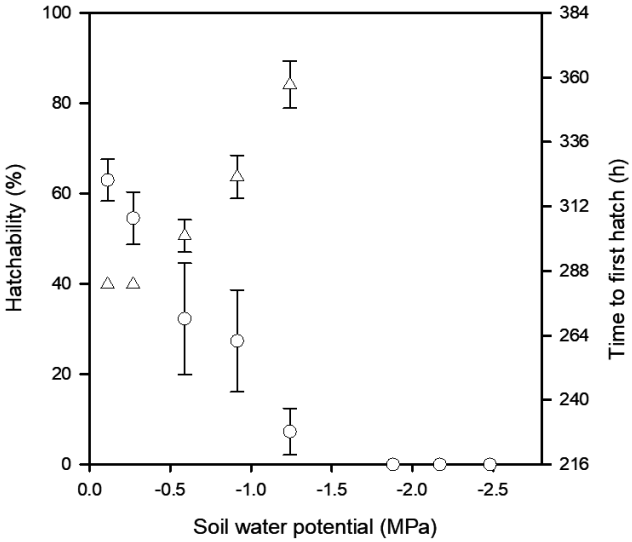

Fig. 3. Hatchability (circles; left y-axis) and time to first hatch (triangles; right y-axis) of *Folsomia candida* eggs after 7-day exposure to varying levels of drought. The values are means ± SE (*N* = 6).

reduce the effective surface:volume ratio and rate of water loss of individual eggs as compared to isolated eggs. Note that the permeability determined here is for isolated eggs. Clustering of eggs by the female may be an adaptive trait in insects and soil-dwelling arthropods that enhances egg survival during drought (Cannon & Block, 1988; Block & Convey, 1995; Clark & Faeth, 1998; Bartlett et al., 2019).

Increasing drought intensity had clear effects on the water content of eggs by the end of the 7-day experiment (one-way ANOVA; F = 40.0; $P < 0.001$; Fig. 2A). Thus, egg water content decreased from 2.5 mg mg^{-1} DW at almost saturated humidity (–0.11 MPa; "control") to about 1 mg mg^{-1} DW at drought levels greater than –1.5 MPa (Fig. 2A). The relative water gain during embryonic development was also significantly reduced when drought levels were increased (one-way ANOVA; F = 68.6; $P < 0.001$; Fig. 2B). The relative water gain decreased linearly with increasing drought levels, but eggs were able to absorb at least some water during their development even at –1.88 MPa (Fig. 2B). Considering that the osmolality of eggs (630 mOsm) is equivalent to a water potential of –1.53 MPa, which is largely the drought level where relative water gain is zero, it may be concluded that the water gain by eggs is entirely based on passive water absorption due to the difference in vapour pressure between eggs and ambient air as described for adult *F. candida* (Bayley & Holmstrup, 1999). Adult springtails can increase their osmolality by synthesis and accumulation of myo-inositol and other compatible osmolytes (Bayley & Holmstrup, 1999; Sjursen et al., 2001; Holmstrup et al., 2015) and it is possible that embryos have the same physiological response to drought. However, chemical analysis (GC-MS) of drought-exposed eggs was unsuccesful in revealing any accumulation of compatible osmolytes, although traces of myo-inositol were found (S. Slotsbo, unpubl.).

Duration of embryonic development (time to first hatch) was significantly prolonged from 12 days in control eggs to ca. 15 days at –1.2 MPa (one-way ANOVA; F = 38.6; $P < 0.001$; Fig. 3). This suggests that relatively small reductions in normal water content (from 2.5 to 1.4 mg mg^{-1} DW; Fig. 2A) will slow embryonic development. Egg survival was significantly reduced from ca. 60% to no survival between –1.2 and –1.88 MPa (one-way ANOVA; F = 19.4; $P < 0.001$; Fig. 3). The relatively low egg survival in control chambers (63% at –0.11 MPa) may indicate that manipulating and placing eggs in tin caps was perhaps killing some eggs since more than 90% of the undisturbed eggs laid on moist plaster of Paris usually survive (Snider, 1973).

The results of the present studies show that eggs of *F. candida* are considerably less drought tolerant than juve-

niles or adult life-stages. Even though *F. candida* has body characters typical of soil dwelling species (no pigmentation or eyes), which are often meso-hygrophilic (da Silva et al., 2012), adults readily survive exposure to soil water potentials at –2.5 MPa, or even down to –3.5 MPa if exposed to gradually increasing drought conditions simulating a natural drought (Sjursen et al., 2001; Holmstrup et al., 2015). This would mean that eggs of *F. candida* would perish if soil water potential in the field approaches the wilting point of plants, which is often reached during summer droughts. The persistence of this species would then depend on the survival of post-embryonic life stages that can give rise to the next generation. Studies have shown that *F. candida* will quickly resume egg laying even after exposure to long and severe drought conditions (Waagner et al., 2011). This is unlike what happens in a number of xerophilic species of springtails, which enter a dormant, anhydrobiotic egg stage during droughts (Poinsot-Balaguer, 1976; Greenslade, 1981). In future studies it would be interesting to study the tolerance of eggs to drought for a range of species of springtails with moisture preferences from xerophilic to hygrophilic.

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