

Effects of spring precipitation on a temperate arable collembolan community analysed using Principal Response Curves

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Abstract

We hypothesized that changes in the pattern of spring precipitation would alter the species composition of a temperate soil-surface collembolan community. Experimental manipulation of precipitation during a drought in southern England was used to test this hypothesis in spring 1997. Replicated plots in a field of spring peas received spring drought (plots shielded from rainfall), reference (actual) rainfall and spring irrigation during the first 2 weeks of May. Shielding plots extended the existing drought to 58 days. Thereafter all plots received natural precipitation only, which in June considerably exceeded the long-term average for the site. Redundancy Analysis (RDA) and the recently-developed method of Principal Response Curves analysis (PRC) were used to summarise and test statistically changes in community composition under the three precipitation treatments, using counts of soil-surface species obtained by suction sampling. Irrigation decreased counts of *Bourletiella hortensis*, but had a positive impact on all other species studied, whilst the effect of spring drought was negative. Effects of spring precipitation persisted for the 97-day duration of the study despite the unusually wet summer. The possibility that changes in patterns of rainfall in northern Europe would promote some species as crop pests is proposed, but not supported by our findings. We use the collembolan data to illustrate some advantages of PRC analysis over RDA and other ordination techniques for analysing community responses to experimental treatments. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

During the last two decades, precipitation in Britain has tended to increase in winter and decrease in summer (Conway, 1998), with an increase in the frequency of droughts (Price, 1998). Other parts of Europe have also experienced a decrease in summer precipitation (Piervitali et al., 1997). Several climate

change models based upon 'business as usual' emissions of greenhouse gases forecast an increase in drought intensity and frequency in south-east England (CCIRG, 1996), most of western Europe (Arnell, 1999) and some other parts of the world (e.g. Fleming and Candau, 1998; Kothavala, 1999). Most of the work investigating potential effects of climate change on arthropods in the UK has so far focused on changes in CO₂ concentration and temperature rather than precipitation (Cannon, 1998), even though changes in patterns of rainfall are thought likely to have a greater effect on the distribution of plants and animals

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than are predicted changes in temperature (CCIRG, 1996).

In Britain, long-term monitoring of biota for determining environmental effects of climate change is being addressed by multi-disciplinary projects such as the Environmental Change Network (Bealey et al., 1998) and component IV of the NERC Terrestrial Initiative in Global Environmental Research (Cummins et al., 1995; Jamieson et al., 1998; Masters et al., 1998; Cummins and Watkinson, 1999), but these studies do not include arable farmland. Arable land occupies a large proportion (ca. 21%) of the land surface of Britain and has a diverse arthropod fauna (Potts, 1991). Collembola are numerically important in arable agroecosystems (e.g. Purvis and Curry, 1980; Röske, 1989; Kováč and Miklisova, 1997) and contribute functionally at several trophic levels to the terrestrial food web (Rusek, 1998). We hypothesized that the species composition of an arable collembolan community would change in response to alteration of precipitation in spring because: (1) collembolan sensitivity to humidity varies interspecifically (e.g. Davies, 1928; Joosse, 1970; Ashraf, 1971; Verhoef and Van Selm, 1983); (2) several species are tolerant to certain conditions of drought (Davidson, 1932; Poinso, 1971; Blancquaert et al., 1981; Alvarez et al., 1999); (3) fungivorous species could potentially be influenced indirectly by effects of precipitation on fungal populations (e.g. Schnürer et al., 1986); (4) herbivorous species could potentially be influenced indirectly by effects of precipitation on foodplants (e.g. Mattson and Haack, 1987); and (5) the timing of rainfall can influence the temporal dynamics of some species (e.g. Davidson, 1932). Synecological studies of collembolan responses to drought and irrigation have been conducted mainly in habitats with a distinct dry season, e.g. in Arctic (e.g. Hodkinson et al., 1998), hot desert (e.g. Whitford, 1992) or semi-arid climates (e.g. Greenslade, 1981), but not in temperate agroecosystems. In this paper we describe the response of an arable soil-surface collembolan community to spring drought and irrigation in southern England in 1997.

The community response was analysed using Redundancy Analysis (RDA) and a relatively new method, Principal Response Curves (PRC) analysis. PRC analysis has advantages over traditional multivariate ordination techniques in that differences between treatments in community composition can be

more clearly visualized than in a conventional ordination diagram whilst retaining interpretation at the level of individual species (Van den Brink and Ter Braak, 1999). Hitherto applied only in aquatic ecotoxicology (Van den Brink and Ter Braak, 1997, 1998, 1999; Kedwards et al., 1999), PRC analysis has potential for wider application in experimental community ecology, which we illustrate with the collembolan data.

2. Materials and methods

2.1. Study site

The study was carried out in 1997 in an 8 ha field of seed peas cv. Eiffel (drilled 17 March) on a commercial farm in Hampshire, southern England (51°7'N 1°2'W). Previous cropping was oilseed rape (cv. Mars) in 1996 preceded by four crops of spring barley (cv. Chariot) (1992–1995). Soil type was a light loam over chalk (Andover series; pH=7.6; saturation capacity=72.5 g water 100 g⁻¹ oven dry soil). Soil composition was 8.4% OM, 8.9% clay, 30.3% silt, 18.3% fine sand, and 10.5% coarse sand.

2.2. Experiment design

Twelve square plots, spaced 2 m apart, each measuring 4 m×4 m and surrounded by a polythene barrier, were set up in the crop on 24 April. The barriers extended 30 cm above and 20 cm below the soil surface to minimise redistribution of mobile arthropod species between experimental treatments. The plots formed a 4×3 grid which was separated from a uniform hedgerow of hawthorn (*Crataegus monogyna* Jacq.) by a gap of ca. 50 m. The location and arrangement of plots was chosen to enable plots to be watered using a nearby irrigation water supply and to accommodate plots between adjacent sets of tractor wheelings. The only pesticides applied to the crop were fomesafen+terbutrin (pre-emergence herbicide, 22 March), lambda-cyhalothrin (insecticide against pea weevils, *Sitona* spp., 1 May) and MCPA+MCPP and cyanazine (herbicides, 15 May). Lambda-cyhalothrin would have temporarily reduced the abundance of some arthropods, but probably not Collembola (Frampton, 1999). These were routine

applications sprayed at label-recommended rates on all plots and are realistic in terms of conventional farming practice.

2.3. Precipitation treatments

Three precipitation treatments were assigned to the 12 experimental plots. Plots were arranged in four blocks, with one replicate of each treatment allocated randomly within each block. The treatments were:

(1) *Reference (actual) rainfall*: The plots received only natural precipitation during the study. Monthly rainfall totals during the study were all below the 20-year site average except during June, when twice the long-term monthly average rainfall fell (Frampton et al., 2000).

(2) *Spring drought*: Plots were manually shielded from rainfall as necessary from 28 April until 12 May using removable polythene covers supported by ropes attached to posts located outside the plots. Thereafter the plots were left permanently uncovered to receive natural rainfall (Fig. 1). Covers were deployed only during rainfall and when in position permitted air circulation through the plots so as to minimise the influence of plot shielding on temperature. Shielding the plots extended an existing 40-day rain-free period by a further 18 days and reduced the precipitation received by drought plots by a total of ca. 36 mm relative to the reference rainfall treatment.

(3) *Spring irrigation*: The plots were watered concurrently using four identical laterally-oscillating garden sprinklers connected in parallel to a pressurized irrigation water supply (total flow rate 14.01 min^{-1}) on 2 May ($40.0 \pm 3.7 \text{ mm}$, duration ca. 1 h) and on 15 May ($22.9 \pm 3.5 \text{ mm}$, duration ca. 40 min). On both occasions irrigation took place between 18:00 and 20:00 hours BST at low wind velocity ($<5 \text{ km h}^{-1}$). Thereafter, spring irrigation plots received only natural rainfall (Fig. 1). We restricted irrigation to periods of low wind speed to ensure that water deposition was homogeneous within experimental plots and to prevent spray drift across non-irrigated plots; high rates were chosen (up to 40 mm in 1 h) to enforce a distinction between experimental treatments, as strong evaporation was anticipated (Marsh, 1996).

The precipitation falling within each plot was measured using a 5-inch diameter rain gauge (UK Meteorological Office standard) sited in the centre of the

plot. Gauges were partially sunk into the soil and adjusted periodically so that the top of each gauge was kept level with the top of the crop foliage.

The drought and irrigation treatments represent extreme cases of spring precipitation in southern England. The 58-day lack of rainfall in the drought treatment would equate to a severe drought in southern Britain, while the irrigation treatment could realistically represent heavy rainfall in May, or crop irrigation (Frampton et al., 2000).

2.4. Arthropod sampling

The work we report here focuses on the soil-surface community of Collembola. We consider this to be an ecologically important cohort of the arable fauna, as surface-active Collembola are widely preyed upon by predatory arthropods (e.g. Sunderland, 1975; Sunderland et al., 1986; Burn, 1992; Nyffeler et al., 1994; Hopkin, 1997). Suction sampling is an efficient method for extracting Collembola from the soil surface (Frampton, 1989), and was used to estimate the abundance of surface-dwelling species. It should be noted, however, that abundance of individual species at the soil surface does not necessarily reflect their overall density in the soil profile, nor the community composition at different depths, which is temporally and spatially dynamic (Hopkin, 1997). This is because some species of Collembola may occupy a wider vertical distribution than others (e.g. Hågvar, 1983); soil structure may influence the penetration of species according to body size (e.g. Marinissen and Bok, 1988); and vertical migration may occur in response to microclimatic conditions (e.g. Whitford et al., 1981; Kampichler, 1990). These aspects of the sampling method are considered when interpreting the results (Section 4).

Counts of soil-surface Collembola were obtained using a 'Ryobi' petrol-driven suction sampler (MacLeod et al., 1994) on 10 occasions, from 1 May to mid-August (−2 to +98 days relative to commencement of the irrigation treatment). The sampler nozzle contained a muslin net with a small mesh ($<100 \mu\text{m}$) to ensure small collembolan instars were trapped. Each suction sample was obtained by placing the sampler nozzle (diameter 11.6 cm) on the ground surface between crop plants for a duration of 10 s at each of five random locations and pooling

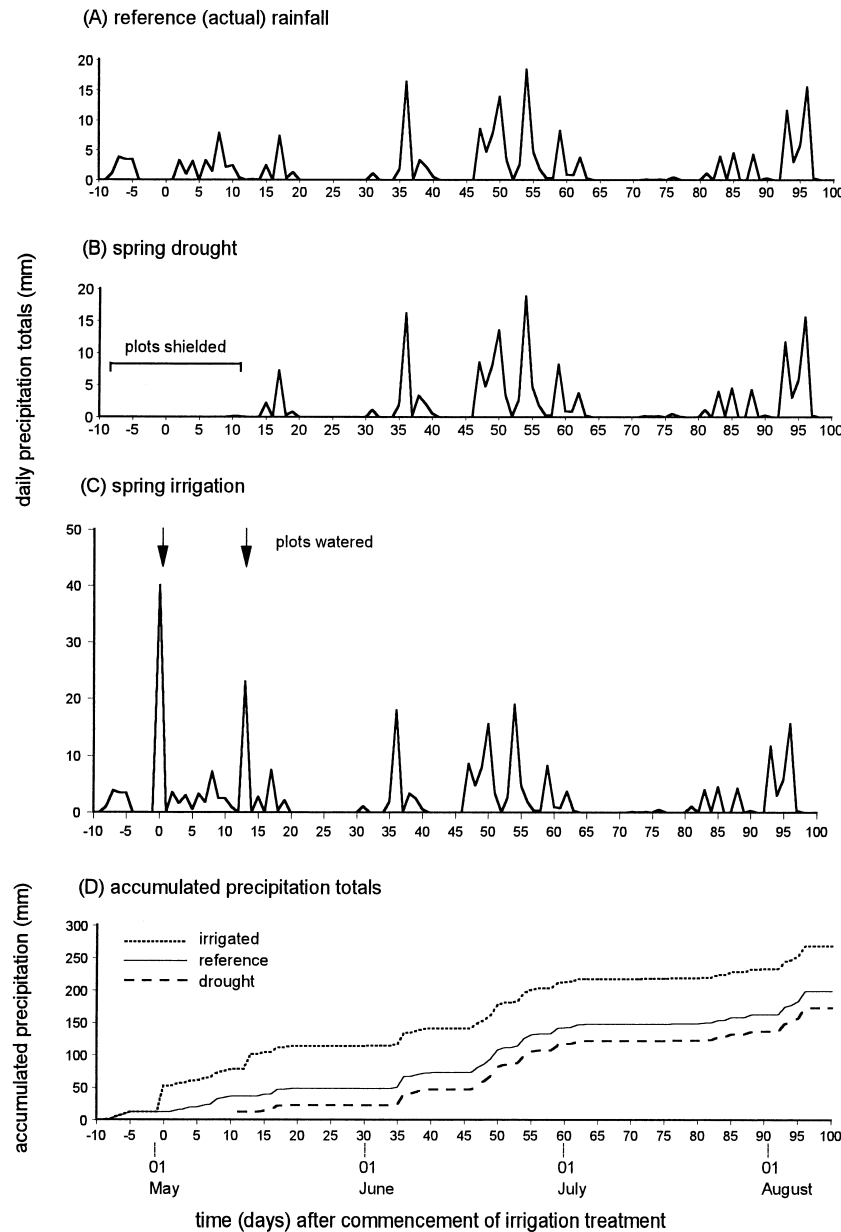


Fig. 1. Precipitation received by the experimental treatments.

the catch. Five samples (each 0.052 m^2) were taken on each sampling occasion and samples were transferred in situ to vials containing 70% methyl alcohol as a preservative. The spatial order of sampling was chosen randomly on each date. To overcome the possibility that understorey vegetation would affect

sampling efficiency, sampling locations were chosen randomly 1 day before samples were due to be taken, and the ground vegetation foliage at each sampling point parted by hand so the sampler nozzle would have unimpeded access to the soil surface. Gaps in the ground vegetation canopy created in this manner were

short-lived as the foliage usually regained its original distribution within 1 week of sampling. Samples were taken only when the soil surface was dry. On each occasion, sampling of all plots was completed within 3.5 h. Arthropods were subsequently separated from plant material and soil by sieving, then Collembola were examined microscopically and, where possible, identified to species (Fjellberg, 1980; Christiansen and Bellinger, 1998). These keys cover Nearctic and Norwegian faunas, respectively, but include species of wider holarctic distribution; other keys to European Collembola which include British species are now considered to be out of date (Rusek, 1995). For each taxon, counts of all instars except eggs were pooled to give an estimate of overall abundance at the soil surface.

2.5. *Vegetation and abiotic variables*

Apart from rainfall totals in each plot, which were recorded daily, for practical reasons it was not possible to sample all crop and abiotic variables on the same dates as arthropods. Random samples of 20 pea plants per plot were used to determine crop growth stage on six dates and mean crop height on seven dates. Vegetation ground cover was estimated using five randomly-placed 50 cm × 50 cm quadrats per plot on each of nine dates. Mean surface soil moisture content was obtained on 12 dates from the mean of two randomly-placed soil samples per plot, of diameter 4 cm and depth 5 cm. Maximum and minimum screen air temperatures above the soil surface were obtained using calibrated thermometers placed 1 cm above the soil under inverted white plastic tubs (14 cm × 17 cm, height 8 cm; sides perforated to permit air circulation).

2.6. *Statistical analysis*

A graphical representation of the temporal response of the collembolan community to the experimental treatments was obtained using the multivariate ordination method RDA. This is the constrained form of PCA (Jongman et al., 1995), meaning that it restricts the ordination to that part of the total variance explained by specified variables. The analysis was based on a method proposed by Van den Brink et al. (1996) for analysing community responses to stress. All levels of

the nominal factors experimental treatment and sampling date were introduced as dummy variables (sensu Ter Braak and Šmilauer, 1998) into the RDA to permit the analysis to focus on the variance attributed to time, treatment, and their interaction. Species counts, x , were transformed to $\ln(x+1)$ prior to analysis to normalize the data (Jongman et al., 1995) and analysed with the software program CANOCO 4 (Ter Braak and Šmilauer, 1998).

Vegetation parameters and abiotic variables were not recorded on the same dates as arthropods were sampled, so they could not be included in the analysis directly as explanatory variables. These factors were instead included as supplementary (passive) variables in the RDA to permit their relationship with the experimental treatments and species responses to be displayed in an ordination diagram; passive variables do not influence the ordination itself but are a means of obtaining an alternative interpretation of already extracted ordination axes (Ter Braak and Šmilauer, 1998).

A problem with traditional ordination methods such as PCA and RDA is that temporal changes in treatment effects (e.g. contrasts with a control) can be difficult to determine where time does not follow a straight line in the ordination diagram (e.g. Van den Brink and Ter Braak, 1997, 1998, 1999; Frampton et al., 2000). PRC analysis is a recently-developed derivative of RDA which overcomes this problem by focusing on the differences between the species compositions of the treatments at each sampling date. This allows the time trajectory of species composition in the control treatment to be displayed as a horizontal line against which deviations in species composition under other experimental treatments can be plotted. The abundance of each species is modelled as a sum of three terms: the species' mean abundance in the control, a date-specific treatment effect and an error. For a given collembolan species k , the effect of treatment d (3 levels) at sampling time t (10 levels) is represented by T_{dtk} . The mean difference between the abundance in irrigation or drought plots (d_1 or d_2) and the control (reference rainfall, d_0) gives a raw estimate of the treatment effect. The response pattern of interest for each species k thus consists of the set of the 3×10 treatment effects (T_{dtk}). PRC analysis models the response pattern of each species, T_{dtk} , as a multiple (b_k) of one basic response pattern (c_{dt}) (i.e. $T_{dtk} = b_k c_{dt}$), which gives the

statistical model for the abundance data

$$Y_{d(j)tk} = Y_{0tk} + b_k c_{dt} + \varepsilon_{d(j)tk} \quad (1)$$

where $Y_{d(j)tk}$ is the abundance of species k in replicate plot j of treatment d at time t , Y_{0tk} is the mean abundance of species k in week t in the control (reference rainfall, d_0), c_{dt} is a basic response pattern for every treatment d and sampling date t , b_k is the weight of each species with this basic response pattern and $\varepsilon_{d(j)tk}$ is an error term with mean zero and variance σ_k^2 . By definition, $c_{0t}=0$ for every t . The least-squares estimates of the coefficients c_{dt} may be obtained from partial RDA (also known as reduced-rank regression with concomitant regressors) (Davis and Tso, 1982; Ter Braak and Looman, 1994). When the coefficients c_{dt} are plotted against sampling date t , the resulting PRC diagram displays a curve for each treatment that can be interpreted as the principal response of the community (Van den Brink and Ter Braak, 1997, 1998, 1999).

The species weight b_k indicates the affinity each individual taxon has with the overall community response as displayed in the PRC diagram. Species weights can be interpreted quantitatively to give the relative abundance under drought or irrigation treatments compared to the control (reference rainfall):

$$\exp(b_k \cdot c_{dt}) \quad (2)$$

gives the fitted difference in abundance of species k under treatment d at time t relative to the control (reference rainfall) treatment (d_0). Where a PRC diagram displays a large proportion of the variation in the data set, the fitted relative abundance of individual taxa inferred from the diagram may closely match the observed relative abundance (Ter Braak and Šmilauer, 1998). Estimates of c_{dt} and b_k were obtained for the Collembola data using the software program CANOCO 4 (Ter Braak and Šmilauer, 1998). The values of c_{dt} were used to plot a PRC diagram to show the overall collembolan community response to the drought and irrigation treatments relative to the reference (actual) rainfall treatment. In Section 3.2 we illustrate the calculation of fitted relative abundance for the individual collembolan species data using the species weights b_k .

The significance of the PRC diagram was tested using Monte Carlo permutation tests, by permuting

whole time series in the partial RDA from which the PRC was obtained using an F -type statistic based on the eigenvalue of the component (Ter Braak and Šmilauer, 1998). The null hypothesis was that the PRC diagram does not display the treatment variance (i.e. $T_{dtk}=0$ for all t , d and k). A second series of permutation tests was performed for each sampling date in which drought and irrigation treatments were tested against the reference to determine whether the differences indicated by the PRC diagram are statistically significant. In each case the null hypothesis was that the principal response under drought or irrigation did not differ from the reference response.

3. Results

3.1. Vegetation and abiotic variables

The experimental treatments applied in May had a short-term effect on soil moisture, which was higher in irrigated plots up to 33 days after plots were first watered but subsequently did not differ between treatments (Fig. 2A). Long-term differences between treatments in crop height (Fig. 2B) and ground vegetation cover (Fig. 2C) persisted to the end of the study; both were consistently lowest under spring drought and highest under spring irrigation. Relatively few records of air temperature at the soil surface are available but they show that 71–97 days after the commencement of irrigation, daily maxima were up to 3°C lower under the irrigated treatment than under drought or reference rainfall whereas daily minima were slightly higher (Fig. 3). Diel temperature range at the soil surface was thus smaller in the irrigated plots than under the other treatments.

3.2. Collembola

Approximately 27,000 Collembola were captured in total, the dominant taxa being *Lepidocyrtus* spp. (32% of the overall catch), *Entomobrya multifasciata* (Tullb.) (18%), *Sminthurinus elegans* (Fitch) (15%), *Pseudosinella alba* (Packard) (14%), *Isotoma notabilis* Schäffer (5%) and *Bourletiella hortensis* (Fitch) (4%). Other taxa recorded were: *Heteromurus nitidus* (Templeton), *Orchesella villosa* (Geoffroy), *I. viridis*

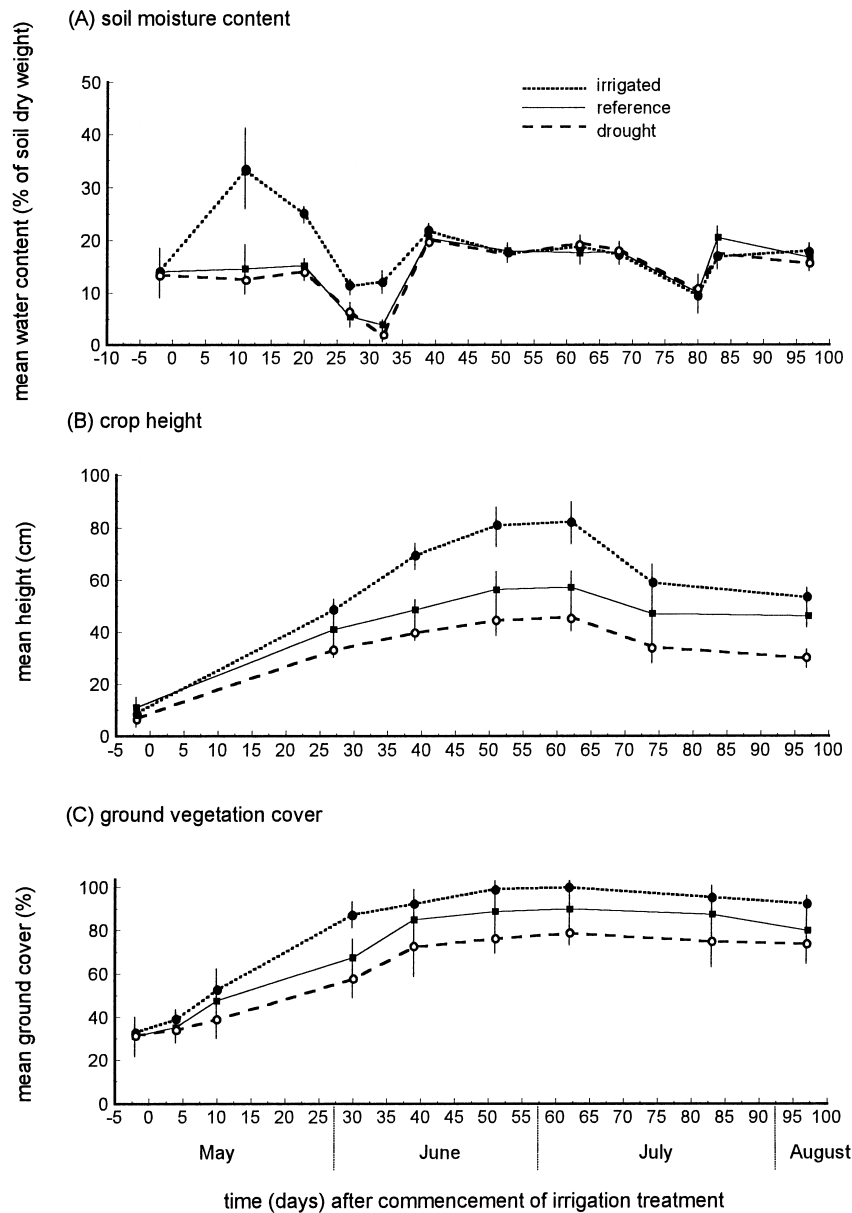


Fig. 2. Influence of the experimental treatments on soil moisture and vegetation. Bars show mean \pm S.D.

Bourlet, *Isotomurus* spp., *Deuterosminthurus* spp., *Sminthurus viridis* (L.), *S. aureus* (Lubbock) and *Sminthuridae*. Counts of all species were initially low and subsequently increased (Fig. 4); Peak catches of Arthropleona were in August (Fig. 4A–F) whereas Symphypleona exhibited peak abundance from May

to early July (Fig. 4G–I). During most of the summer, species richness at the soil surface was lowest in drought plots and highest in irrigated plots (Fig. 4L). Surface counts of most taxa were usually highest under the irrigated treatment, but in June and July *B. hortensis* counts were lowest in irrigated plots (Fig. 4I).

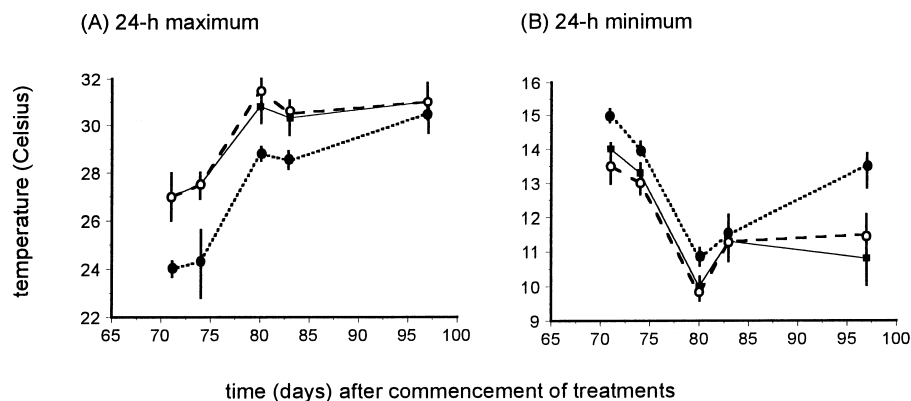


Fig. 3. Mean ($n=3$) screen air temperature (°C) recorded 1 cm above the soil surface in field peas subjected to reference rainfall (—■—), spring drought (---○---) and irrigation (---●---). Bars show range of readings.

RDA scores for samples and species were plotted separately for clarity (Fig. 5A and B). The analysis is restricted to that part of the total variance (67%) which is explained by treatment and sampling date, plus their interaction. Of this variance, 80% is displayed in the ordination diagram, 62% being explained by the first axis and 18% by the second axis. Several patterns are evident in the RDA ordination diagram (Fig. 5): (1) Samples taken early in the study lie mainly in the left half of the diagram, but a shift in the position of sample points towards the top right quadrant is discernible as time progressed (i.e. the time trajectory of samples is not linear in the diagram). Because most species are placed on the right hand side of the diagram, this shift indicates a general increase in abundance with time. (2) Differences between treatments in species composition generally increased over time, as indicated by the separation of time-trajectories (dashed lines in Fig. 5A) towards the end of the study. (3) The position of the sample points later in the study (Day +68 onwards) correlates closely with the vector of accumulated rainfall in the diagram. (4) Species points were either close to the origin, indicating little influence of the treatments on collembolan counts, or mirrored the distribution of sample scores for the irrigated treatment, indicating a positive influence of irrigation on abundance; the opposite pattern (indicating a negative effect of irrigation on abundance) was evident only for *B. hortensis* (Fig. 5B). (5) Except near the origin, species points for *Arthropleona* and *Symphyleona* (Fig. 5B) form discrete groups in the ordination dia-

gram. This reflects differences in the timing of peak counts (*Symphyleona* earlier than *Arthropleona*).

The ordination diagram shows which species and variables contributed most to the effects of treatment, time and their interaction, but the temporal change in treatment effects for the whole collembolan community is difficult to follow (Fig. 5). Changes in treatment effects through time are more clearly shown in the PRC diagram (Fig. 6A). Sampling date accounted for 43% of the total variance of the data set and treatment 24%, with a significant proportion (65%) of the treatment effects variance being displayed in the PRC diagram ($p < 0.005$). The PRC diagram shows that species composition was initially similar but changed when the treatments were applied (Fig. 6). Differences relative to the reference treatment were consistent in direction throughout the season (values of c_{dt} for drought and irrigation are not randomly placed around the reference), and were still evident at the last sampling date (Day 97). Results of permutation tests show that the largest effects of drought and irrigation relative to the reference, and the largest differences between drought and irrigation, were statistically significant (Fig. 6). Effects of drought as displayed in the PRC diagram are smaller and less persistent than those of irrigation, consistent with differences in the amount of precipitation each treatment received (Fig. 1D).

The positive species weight for *S. elegans* indicates this species to have a positive relationship with the PRC diagram (Fig. 6B). The fitted relative abundance of *S. elegans* in irrigated plots at Day

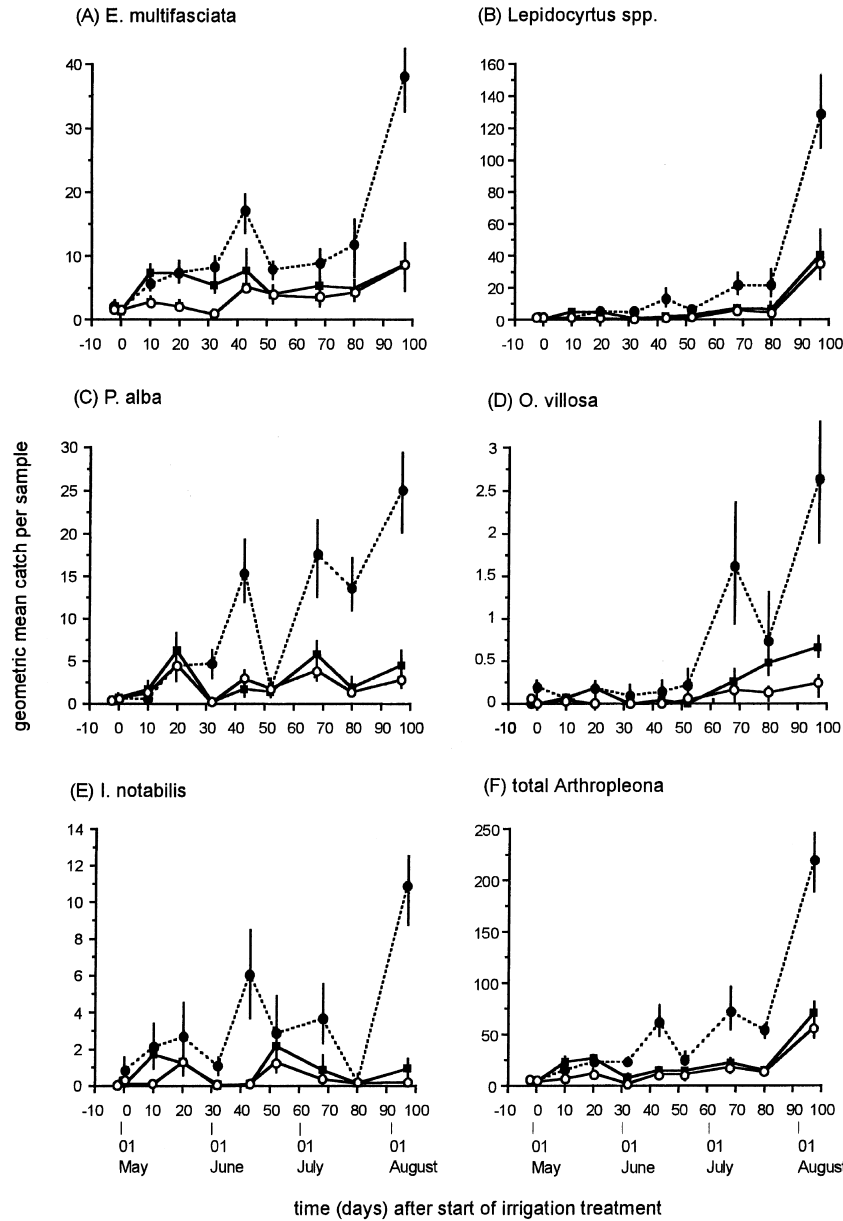


Fig. 4. Geometric mean ($\pm 95\%$ C.I.) abundance (A–K) and species richness (L) of Collembola under reference rainfall (—■—), drought (---○---) and irrigation (---●---) treatments. Note different abundance scales.

43 (from Fig. 6 and Eq. (2)) is $\exp(1.56 \times 2.1) = 26.5$ times the abundance under reference rainfall. For *B. hortensis* the fitted relative difference in abundance between reference and irrigated plots at Day 43 is $\exp(1.56 \times -0.74) = 0.32$. The PRC analysis thus pre-

dicts a relative abundance of *B. hortensis* under irrigation which is ca. 30% of its geometric mean count under reference rainfall. These fitted values agree well with observed differences between treatments (Fig. 4G, I).

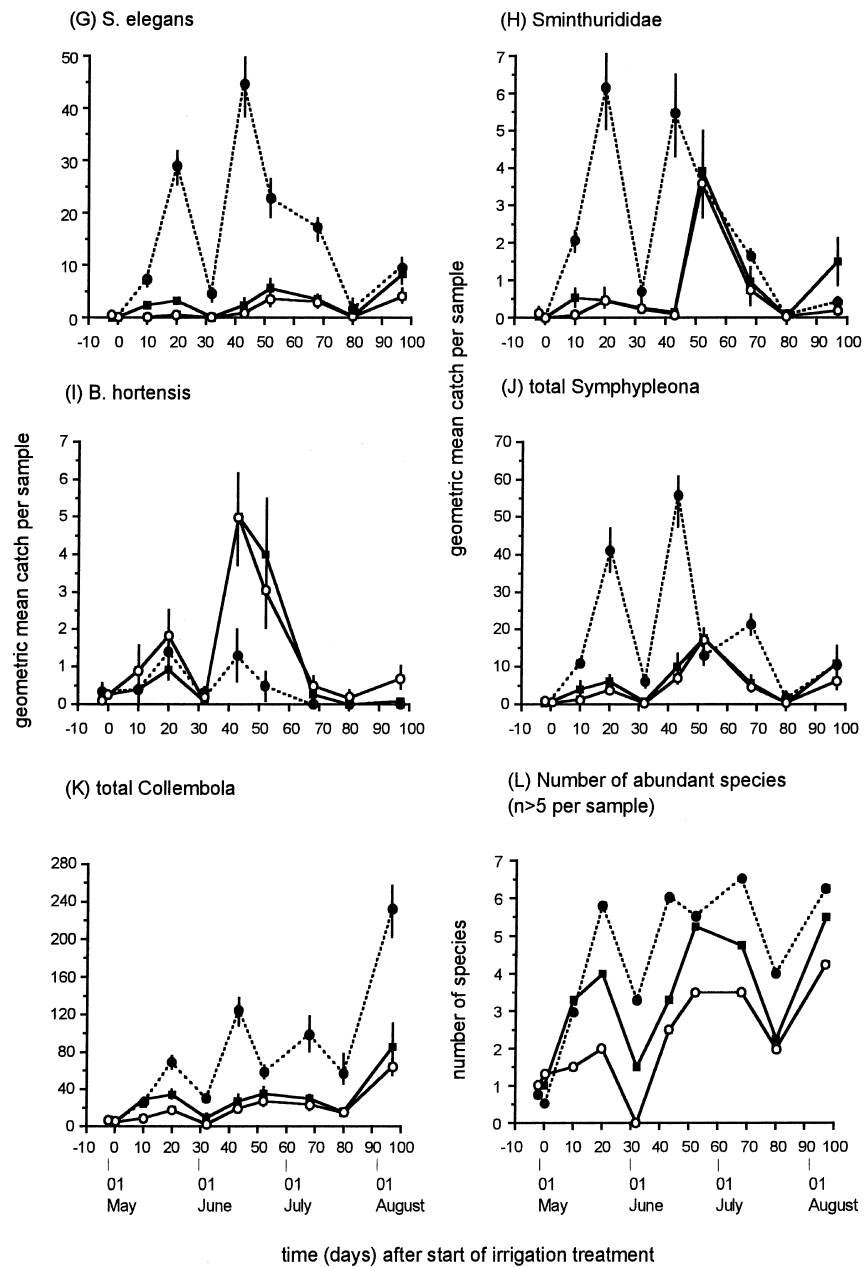


Fig. 4 (Continued).

4. Discussion

4.1. Experimental design

Our study was carried out during prevailing drought conditions in spring 1997 so that precipitation could

be manipulated by watering experimental plots. As less rainfall than usual fell during spring 1997, the reference (actual) rainfall treatment itself equates to a drought treatment, albeit less severe than the enforced spring drought with which it was contrasted (40 and 58 consecutive rain-free days respectively). Comparing

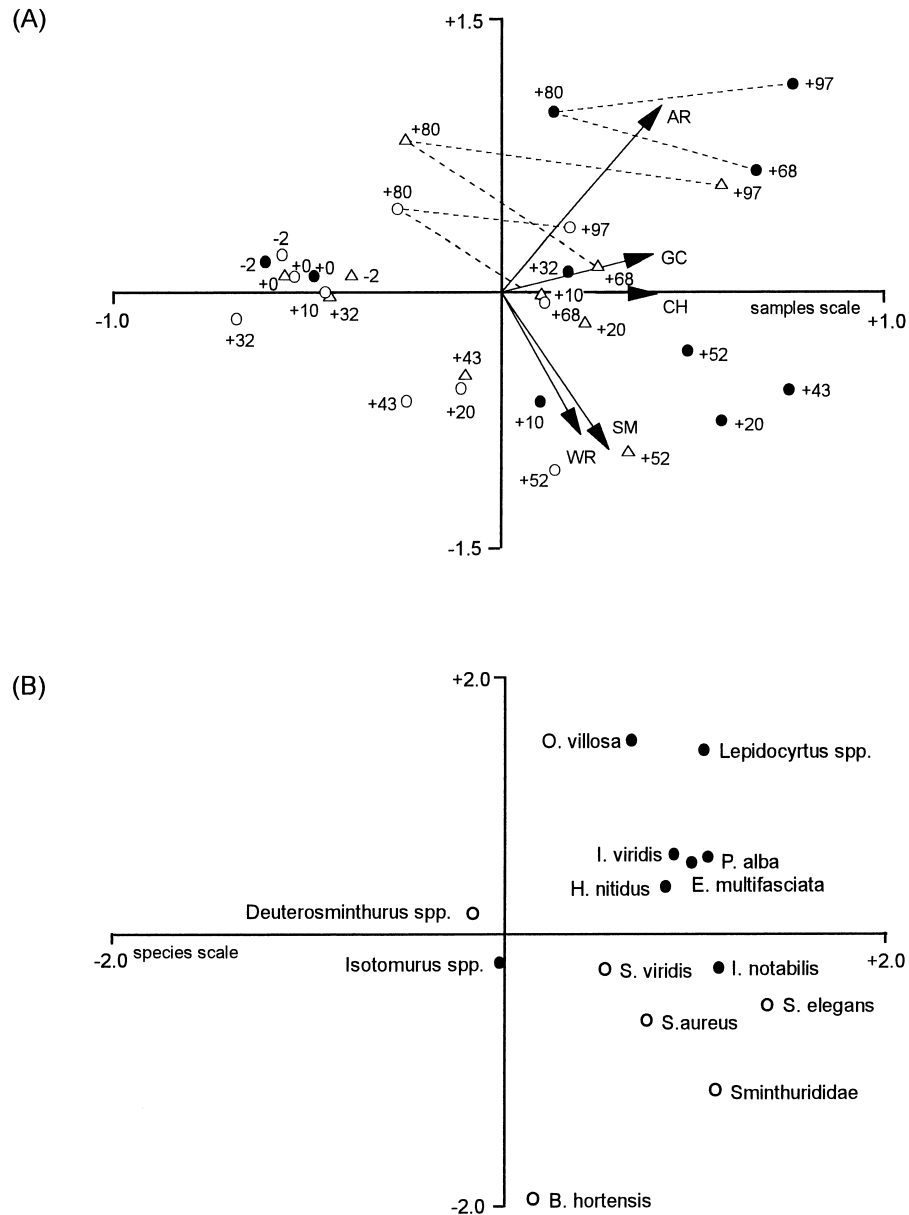


Fig. 5. RDA ordination diagrams. (A) Sample scores for reference rainfall (Δ), spring drought (○) and spring irrigation (●); numbers indicate days relative to start of irrigation treatment. Dashed lines show time-trajectories of treatments from Days +68 to +97. Arrows show the supplementary variables: accumulated rainfall (AR), crop height (CH), ground cover (GC), soil moisture (SM) and rainfall in the week (7 days) preceding sampling (WR). Scale for supplementary variables=2.0×samples scale. (B) Species scores for orders Arthropleona (●) and Symphypleona (○).

effects of drought and irrigation against the reference rainfall treatment could thus underestimate the impact of drought, and exaggerate that of irrigation relative to conditions which would be more 'typical' of spring

precipitation. Nevertheless, differences in abundance were clearly evident between all three treatments, and the contrast between drought and irrigation treatments gives an indication of the range of variation in colle-

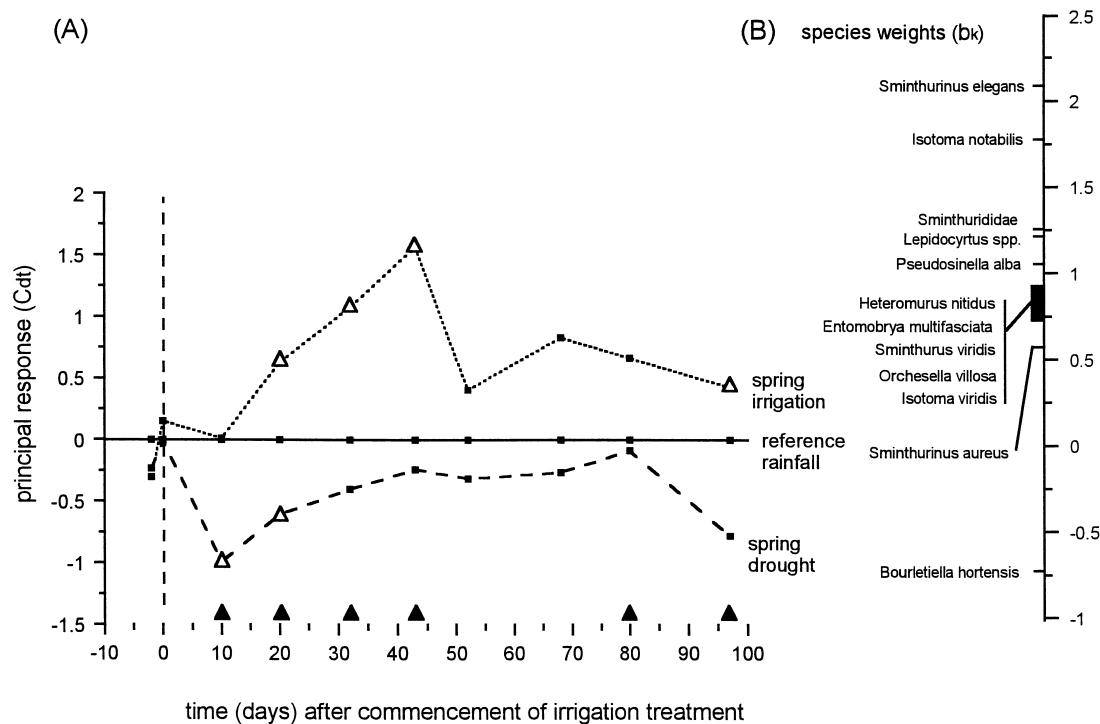


Fig. 6. (A) Principal Response Curves (PRC) diagram showing the response over time of a collembolan community to manipulated spring rainfall treatments. (B) Species weights indicating the relative contribution of individual species to the community response displayed in the PRC diagram. Triangles denote significant differences ($p < 0.05$) relative to the reference treatment (Δ) or between drought and irrigation treatments (\blacktriangle).

bolan abundance which could result from year-to-year changes in spring precipitation.

The focus here is on the community-level response of Collembola to the precipitation treatments, but the experimental design would also have been appropriate for investigating individual species' responses using univariate analysis of variance (ANOVA). A repeated measures model would be applicable as each plot was sampled repeatedly during the season, but an underlying assumption is that there is no interaction between time (i.e. sampling date) and other variables such as treatment or block (Underwood, 1997). If this assumption is invalid, the ANOVA cannot test for differences among treatments. Instead, separate tests for treatment effects within sampling date are recommended (Underwood, 1997), with appropriate adjustment of the F -ratios to reduce the probability of Type I errors associated with multiple tests (e.g. Sokal and Rohlf, 1995). The overall number of tests will, however, depend not

only on the number of sampling dates but also on the number of response variables (i.e. species) to be tested. Where there are many species (e.g. 189 in Van den Brink and Ter Braak, 1999), multiple testing with univariate methods is clearly not a practical option. Multivariate ANOVA offers a possible alternative but requires a higher sampling effort and is limited in the number of response variables that can be analysed (e.g. Hair et al., 1995). RDA and PRC, which are not subject to these restrictions, can usefully identify species whose responses warrant a more detailed (e.g. univariate) analysis without the need for multiple testing. Thus, the atypical response of *B. hortensis* to the irrigation treatment in mid-June indicated by PRC analysis may be tested ad hoc, e.g. with a two-way ANOVA (treatment fixed, block random); the effect of irrigation in mid-June is significant ($F_{1,32} > 13$; $p < 0.01$), with no evidence for treatment \times block interactions ($F_{6,32} < 2$; $p > 0.3$).

4.2. Sampling considerations

Suction sampling was carried out when the soil surface was dry to touch but in fact soil moisture to a depth of 5 cm differed between precipitation treatments up to Day 33 (Fig. 2). No consistent differences were evident between the treatments in the dry weight of soil in suction samples (G.K. Frampton, unpublished data), suggesting that sampling efficiency was not affected by the differences in soil moisture. Samples could not be taken when the soil surface was wet, but this is unlikely to have biased the results strongly because surface soil dried quickly following rainfall events, meaning that dry soil surface conditions predominated during the study (soil moisture content in the top 5 cm was mostly $\leq 20\%$; Fig. 2A).

4.3. Advantages and limitations of Principal Response Curves

The RDA ordination (Fig. 5) graphically summarizes a complex data set but is difficult to interpret in terms of the persistence of treatment effects. PRC analysis on the other hand provides a concise summary of the temporal dynamics of the treatment effects which, in combination with permutation tests (Fig. 6), clearly shows that effects of the spring treatments persisted through the season, despite the wet summer conditions in June. Because 30 separate permutation tests were performed, each with a Type I error rate of 5%, two of the significant treatment effects displayed in the PRC diagram might be explained by chance. This does not substantially affect our interpretation of the PRC diagram, however, as we make no attempt to draw inferences from the outcome of individual permutation tests. In studies where the results of individual tests are of interest, the Type I error rate may be reduced by adjusting the significance level at which each test rejects the null hypothesis (e.g. Sokal and Rohlf, 1995).

The response curve for the reference treatment in a PRC diagram coincides with the horizontal axis of the diagram, meaning that the number of curves displayed is one fewer than the number of treatment levels. This contributes to the clarity of the diagram. At least five treatment levels (including reference) can be displayed in a PRC diagram without loss of visual clarity (Van den Brink and Ter Braak, 1999; Van den Brink et al., 2000). Though PRC analysis

has been applied so far only in aquatic ecotoxicology, our analysis of the collembolan community illustrates the potential of this technique for wider application in experimental community ecology. PRC analysis is applicable to any investigation of temporal changes in species composition in response to two or more experimental treatments, but for statistical interpretation of treatment effects within dates the treatments must be replicated adequately for permutation testing. PRC analysis also has potential as a tool in long-term ecological monitoring where replication of experimental treatments is not feasible, provided that care is taken to avoid pseudoreplication (Frampton, 2000a).

The PRC diagram enables the start and end (i.e. recovery) points of a community response to experimental treatments to be determined, which may not be possible using other analytical approaches (see for example, the complexity of Figs. 4 and 5). We could define recovery as the point in time after which c_{dt} (the size of the treatment effect) consistently remains below a nominated deviation from the reference treatment. Such a deviation could be chosen arbitrarily yet still have value for comparative purposes if applied consistently to different data sets. Another possible yardstick for determining the start of community recovery using PRC analysis is the point in time at which differences of c_{dt} from the reference treatment cease to be statistically significant (e.g. Van den Brink and Ter Braak, 1999). Lack of synecological information on Collembola in arable habitats makes it difficult to determine the ecological importance of treatment effects, so setting a precise threshold value of c_{dt} against which to judge start and end points of effects is not particularly meaningful for our data. The PRC diagram does however suggest that the irrigated community had not fully recovered by the last day of the study whereas effects of drought were less persistent; persistent differences between the drought and irrigation treatments are also evident. Using values of c_{dt} against which to judge community recovery is most likely to have value in studies with other biota where the wider ecological implications of treatment effects are more tangible, e.g. where a numerical relationship between macroarthropod abundance and the survival rates of insectivorous wildlife has been established.

Siepel et al. (1989) demonstrated the potential value of multivariate methods for identifying indicator

species or taxa (whose abundance may be indicative of particular environmental variables or experimental treatments). They suggested that indicator species could be defined as those which explained more than 30% of the variance on a given canonical axis (the highest proportion of the treatment effects variance explained by a species in our study was 26.3% for *S. elegans*). In PRC analysis the species weights b_k may be used for this purpose: species with the highest weight (in our case, *S. elegans*) are most likely to follow the overall community response. We have excluded from the PRC diagram those species with low weights (values of b_k in the range -0.5 to $+0.5$) as they have a low affinity with the overall community response, meaning that their response is either weak (e.g. due to low abundance), or unrelated to that indicated in the PRC diagram (Van den Brink and Ter Braak, 1999). Numerically important species could in theory have low species weight if their response pattern is unrelated to that shown in the PRC diagram but such a situation can be identified easily by checking the counts of taxa with low weights. In our case, taxa excluded on the basis of low weights were all rare in samples.

4.4. Collembolan responses to precipitation

With the exception of *B. hortensis*, collembolan abundance was increased by irrigation and decreased by drought, and a similar response pattern occurred among macroarthropods (e.g. Araneae, Coleoptera, Hemiptera, Diptera, Hymenoptera) (Frampton et al., 2000). It is not possible from our data to determine causal mechanisms, but two general points emerge from the data which may be instructive in terms of ecological processes. The first point is that the species which increased markedly in abundance soon after dry plots were irrigated all belong to the order Symphypleona. Species of Symphypleona are known to exhibit synchronised hatching when rainfall follows drought (e.g. Davidson, 1932; Wallace, 1967) and it is notable that watering of arable soils in a recent laboratory study led to synchronised hatching only of Symphypleona, not Arthropleona (Alvarez et al., 1999). Symphypleona exhibited a stronger relationship with soil moisture than with crop height or ground cover (cf Figs. 2, 4, 5) which would be consistent with several possible effects of soil moisture,

e.g. stimulation of hatching, the activation of anhydrobiotic nymphs, or vertical migration in response to favourable moisture conditions at the soil surface (e.g. Whitford et al., 1981; Kampichler, 1990). Soil moisture could also have acted indirectly via effects on soil fungi (e.g. Schnürer et al., 1986), which are important in the collembolan diet (e.g. Hopkin, 1997). The reason why *B. hortensis* responded differently to all other taxa is not known; further work would be needed to establish whether the adverse effect of irrigation on this species is a general phenomenon in other arable crops. The second general point emerging from our results is that treatment effects among some taxa, particularly of Arthropleona, persisted through the summer despite the relatively short-term manipulation of precipitation in May and the fact that June was exceptionally wet. Such persistence of effects could reflect indirect effects of the precipitation treatments upon vegetation (references in Frampton et al., 2000). The potential complexity of interactions is illustrated by the fact that spring precipitation affected vegetation growth which in turn influenced the diel temperature range at the soil surface up to 97 days after the initial treatment manipulation. Differences in temperature between the treatments would in turn probably have affected collembolan growth, if not also survival (e.g. Hopkin, 1997).

It was not possible to reliably measure the humidity to which Collembola were exposed in our study. However, three of the species captured are known to differ in their susceptibility to low humidity (Davies, 1928). These are *I. viridis* (most susceptible), *E. multifasciata* and *S. viridis* (least susceptible). Their susceptibility to the precipitation treatments would be expected to differ if humidity was a limiting factor. The distribution of species scores in the RDA ordination does suggest that *I. viridis* was more closely associated than *S. viridis* with the irrigation treatment but does not identify the causal mechanism. Despite their sensitivity to low humidity, both these species can tolerate some types of drought (see below).

Irrespective of the causal mechanisms, the differences between treatments in the abundance of Collembola at the soil surface have implications for the availability of Collembola in the diet of ground-foraging predators. Low collembolan abundance under the drought and reference treatments is of particular concern, as a number of farmland arthro-

Pods such as *Stenus* spp. (Staphylinidae), *Leistus* spp. and *Notiophilus* spp. (Carabidae) are stenophagous predators of Collembola. Many polyphagous arthropods also have a collembolan diet (e.g. Sunderland, 1975; Sunderland et al., 1986; Burn, 1992; Nyffeler et al., 1994; Hopkin, 1997) so effects of the precipitation treatments on some predators (Frampton et al., 2000) could reflect a response to collembolan abundance. The importance of predation for determining effects of the precipitation treatments at the community level is difficult to establish from our data but could be investigated in future manipulative studies of precipitation effects by measuring removal of prey baits (e.g. Burn, 1992).

4.5. Drought tolerance and pest status

Of the species we trapped, three are known to exhibit summer drought tolerance in drier (e.g. Mediterranean) climates: *I. viridis* (Poinso, 1971), *S. aureus* (Blancquaert et al., 1981) and *S. viridis* (Davidson, 1932). Recent work has also shown that *B. hortensis*, *S. elegans* and *S. viridis* survived simulated spring drought in southern England (Alvarez et al., 1999). Collembola are not serious pests of field crops in northern Europe but several of the species we trapped (e.g. *S. viridis* and *B. hortensis*) can cause significant crop damage in drier climates (Ireson, 1993; Bishop et al., 1998), as outbreaks may be triggered by synchronised hatching when rainfall follows drought (e.g. Wallace, 1967). Manipulation of precipitation under laboratory conditions has recently provided evidence that rainfall-induced synchronised hatching of these species would also occur in arable soils of northern Europe following certain conditions of spring drought (Alvarez et al., 1999). This raises the question of whether an increase in the frequency or severity of droughts would promote these species as pests in northern Europe. In our study the drought and reference treatments both effectively represent different degrees of drought in early May (Section 4.1), terminated by rainfall in late May and June (Fig. 1). Counts of *B. hortensis* under these treatments were generally low until Day +43, when an increase followed the first substantial rainfall event of the summer (cf Figs. 1 and 4). However, even at peak abundance, counts of *B. hortensis* were generally low and our data provide no evidence that any other species were favoured by the

drought treatment at any time in the season. Although irrigation increased the abundance of most species, no Collembola appeared to pose any threat to the pea crop following any of our manipulations of precipitation, as very few were found on the pea plants after flowering.

4.6. Implications and recommendations

Overall, the soil surface collembolan community was favoured by spring irrigation but it is unlikely that our results would be representative of a euedaphic community, whose fauna would be exposed continuously to a saturated atmosphere. For instance, Shaddy and Butcher (1977) observed no effect of irrigation on the soil dwelling collembolan *Tullbergia granulata* Mills. Our results are also unlikely to be representative of drought effects in autumn-sown crops whose growth would be less critically dependent upon spring precipitation. The persistence of treatment effects in a spring-sown crop for up to 3 months during an atypically wet summer shows that a short-term adjustment of spring precipitation may substantially influence summer soil-surface collembolan abundance irrespective of subsequent weather conditions (the largest impact of irrigation on some species of Arthropleona occurred 80 days after spring irrigation ceased). Spring precipitation could thus account for some of the large year-to-year fluctuations in collembolan abundance seen in arable rotations which contain spring-sown crops (Frampton, 2000b). Our precipitation treatments clearly represent a small fraction of all possible intensities and frequencies of rainfall occurrence in spring, so further studies of the effects of precipitation on temperate arable arthropods would be desirable. This is because (1) patterns of precipitation are anticipated to be an important component of changing climate, and (2) the response of the temperate arable fauna to climate change is not currently being addressed by any large-scale monitoring studies. There is evidence that the diet of predatory arthropods may alter in response to availability of collembolan prey (e.g. Burn, 1992), so the question of whether the magnitude of changes in collembolan abundance we report here would substantially affect the predator fauna in the longer term (e.g. following successive droughts) needs to be addressed.

5. Conclusions

In a temperate spring-sown arable crop, spring rainfall and irrigation are important determinants of the abundance of Collembola at the soil surface throughout the crop season. Substantial differences in summer collembolan abundance would be expected between years with high and low spring rainfall, but the implications for predators of Collembola requires further investigation, particularly as some are important in the diet of declining farmland birds. PRC analysis proved to be capable of concisely summarising the complex data set of the collembolan community whilst permitting information to be displayed which could not have been readily obtained from a traditional ordination diagram. The technique is directly relevant to community ecology and the visual clarity of PRC diagrams makes them a potentially valuable tool for presenting complex ecological information to non-experts.

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