

# Effects of spring drought and irrigation on farmland arthropods in southern Britain

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## Summary

1. Information is lacking on how possible future changes in the seasonal occurrence and intensity of precipitation in Europe will affect the arthropod community of arable farmland.
2. We used a novel experimental approach to investigate the responses of farmland arthropods to spring precipitation in a spring-sown legume. Replicated plots were subjected to spring drought (plots shielded from rainfall), actual rainfall (reference) and spring irrigation. Shielding plots extended an existing drought to 58 days.
3. The response of epigeic arthropods was investigated using principal components analysis (PCA) and principal response curves (PRC). Temporal changes in treatment effects at the community level were more clearly displayed by PRC than by PCA, while PRC improved the interpretation of individual species' responses. PRC analysis has potential for wider application in ecological experiments and monitoring.
4. Short-term manipulation of precipitation in May affected the arthropod community for at least 97 days, despite exceptionally high rainfall in June. The effects of drought on the abundance of herbivores, mycophages, omnivores and predators were negative, while those of irrigation were positive. There were no differences in the responses of beneficial and pest taxa.
5. In addition to their intrinsic importance, these findings illustrate that spring weather might affect the availability of arthropod prey for insectivorous wildlife. Food availability has been implicated in the population declines of several insectivorous farmland birds.
6. The difficulty of manipulating rainfall in a temperate climate precludes realistic field studies of how farmland arthropods respond to precipitation. We suggest that automated rain shielding of experimental plots provides a technique for wider application in drought studies.

*Key-words:* climate change, community ecology, invertebrates, multivariate analysis, principal components analysis, principal response curves.

*Journal of Applied Ecology* (2000) **37**, 865–883

## Introduction

Annual precipitation in southern Europe has declined since 1951 (Piervitali, Colacino & Conte 1997). The past two decades have seen precipitation in Britain increase in winter and decrease in summer

(Marsh 1996; Conway 1998), with four droughts during the past 25 years of a severity that would be expected only once in 200 years or more (Price 1998). Considerable uncertainty is associated with projected future changes in precipitation (Parry 1992) but there are indications that the intensity and frequency of droughts will increase across south-east Britain (CCIRG 1996), most of western Europe (Arnell 1999) and other regions such as eastern Aus-

tralia (Kothavala 1999) and Canada (Fleming & Candau 1998). So far, understanding of the likely ecological consequences is limited.

Changes in patterns of rainfall are likely to have a greater effect than are changes in temperature on species' distributions (CCIRG 1996), especially among rare species (Elmes & Free 1994). Most work investigating the potential effects of climate change on arthropods in Britain has focused, however, on the effects of changes in CO<sub>2</sub> concentration and temperature rather than precipitation (Cannon 1998). Predicting the effects of precipitation on arthropods is difficult because forecasts have low spatial resolution and high regional uncertainty (Houghton *et al.* 1996) and because soil water availability influences complex ecological interactions in food webs (Mattson & Haack 1987; Whitford 1989; Fox *et al.* 1999). An alternative to the predictive approach is to measure directly the responses of arthropod communities to simulated climate change. Such an approach has been employed in short-term studies of soil arthropods in habitats with a distinct dry season, for example hot desert (Whitford *et al.* 1981), semi-arid lands (Greenslade 1981) or the Arctic (Hodkinson *et al.* 1998), but little information exists on arthropod community responses to precipitation in temperate ecosystems (Whitford 1992), where the unpredictability of precipitation does not favour short-term manipulations. Recently, multidisciplinary projects such as the Environmental Change Network (Bealey, Howells & Parr 1998) and the NERC Terrestrial Initiative in Global Environmental Research (TIGER; Cummins *et al.* 1995; Cummins & Watkinson 1999) have started to address the need for long-term biological monitoring to provide comprehensive quantitative data on effects of temperate climate change, but these projects do not include arable ecosystems.

Arable land is ecologically important in terms of its diverse arthropod fauna and area (Potts 1991). In Britain, arable crops occupy approximately 4.8 million ha (Thomas, Garthwaite & Banham 1997), which is one-fifth of the land area and considerably exceeds that of all designated nature reserves (Potts 1991). Arable farmland arthropods are valued as natural enemies of insect pests (Sunderland *et al.* 1997; Marc, Canard & Ysnel 1999), as potential indicators of habitat condition (Fauvel 1999; Iperiti 1999; Paoletti 1999) and as important food for insectivorous wildlife, including declining farmland birds (Potts 1986; Wilson *et al.* 1999; Borg & Toft 2000). Concern has been expressed about declines in the abundance and diversity of arthropods on arable land (Sotherton 1998; Ewald & Aebischer 1999; Kromp 1999) but little is known about the contribution of climatic factors, nor how arable arthropods might respond to predicted changes in precipitation.

In 1997 persistent dry weather during March and April in southern England provided an opportunity

to investigate the reaction of the arable fauna to different intensities of manipulated spring precipitation, including drought. We controlled the precipitation received by experimental plots in a spring-sown crop and subsequently monitored the effects on the abundance of epigeic arthropods using suction sampling. Principal components analysis (PCA) and principal response curves (PRC) (van den Brink & ter Braak 1998, 1999) were used to analyse temporal changes in the community response to different precipitation treatments. The PRC approach has hitherto been used only in aquatic ecotoxicology, but has some advantages over other ordination techniques which we illustrate with these terrestrial arthropod data.

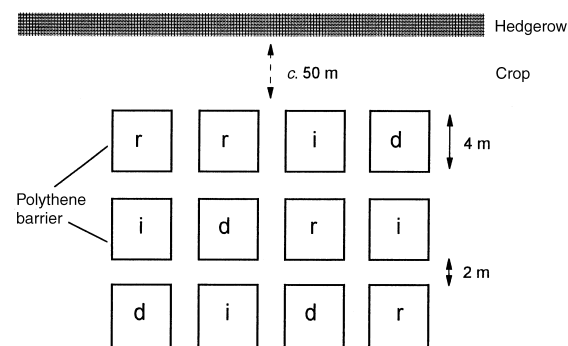
## Methods

### STUDY SITE

The study was carried out in 1997 in an 8-ha field of seed peas (cultivar Eiffel) on a commercial farm in Hampshire, southern England (51°7'N 1°2'W). Soil type was a light loam over chalk (Andover Series, pH = 7.6) comprising 8.4% organic matter (OM), 8.9% clay, 30% silt, 18.3% fine sand and 10.5% coarse sand. Sowing date (17 March) was in the first week of a 42-day period of dry weather. Rainfall in the 16 days prior to sowing had averaged 1.3 mm day<sup>-1</sup>, which is below the 10-year average for the site in early March (1.9 mm day<sup>-1</sup>, 1985–96 data).

### EXPERIMENTAL TREATMENTS

Twelve 4 × 4-m square plots, spaced 2 m apart and each enclosed by a polythene barrier (height 30 cm; depth below soil 20 cm) to minimize dispersal of arthropods between plots, were set up in the crop on 24 April 1997 (Fig. 1). A rain gauge (UK Meteorological Office, Bracknell; 5-inch standard) was installed at the centre of each plot and its depth



**Fig. 1.** Spatial arrangement of reference (actual) rainfall (r), spring drought (d) and spring irrigation (i) treatments applied to replicated plots in spring peas.

in the soil adjusted periodically to ensure that the top of the gauge remained level with the top of the crop. Three precipitation treatments were applied randomly within each of four blocks of the experimental plots, giving four replicates of each treatment (Fig. 1). The three treatments were as follows. (i) Reference rainfall: plots received only natural precipitation throughout the study. (ii) Spring drought: plots received only natural rainfall except during the period 28 April–12 May inclusive, when polythene covers were deployed manually to shield plots from rainfall. Covers were used only during rainfall, and when in use were supported by ropes in such a way that ambient air was permitted to circulate underneath to minimize the influence on temperature. (iii) Spring irrigation: plots received  $40.0 \pm 3.7$  mm irrigation on 2 May (duration *c.* 1 h) and  $22.9 \pm 3.5$  mm on 15 May (duration *c.* 40 min), but at all other times received only natural precipitation. On each irrigation occasion the four plots were watered simultaneously between 18.00 and 22.00 British Summer Time (BST) at low wind velocity ( $< 5 \text{ km h}^{-1}$ ) using identical laterally oscillating garden sprinklers connected to a pressurized farm irrigation supply (total flow rate  $14.01 \text{ min}^{-1}$ ). As the study was conducted in a commercial crop, several pesticides were applied at label-recommended rates: fomesafen + terbutrin (pre-emergence herbicide on 22 March), lambda-cyhalothrin (synthetic pyrethroid insecticide against *Sitona* spp. pea weevils on 1 May) and MCPA + MCPP and cyanazine (herbicides on 15 May). Each application was made simultaneously to all plots.

#### ARTHROPOD SAMPLING

A petrol-driven 'Ryobi' suction sampler (Ryobi Power Equipment (UK) Ltd, Quedgeley Glos., UK) (MacLeod, Wratten & Harwood 1994) with an 11.6-cm diameter nozzle containing a muslin net (mesh  $< 100 \mu\text{m}$ ) was used to sample surface-dwelling arthropods on 10 occasions from 1 May to crop harvest (12 August) ( $-2$  to  $+97$  days relative to the first irrigation treatment). Each sample was obtained by placing the nozzle on the ground between crop plants for 10 seconds at each of five random locations within the plot, excluding the peripheral 0.5 m, and pooling the catch. Care was taken to minimize any effect of ground vegetation cover on sampling efficiency by sampling soil rather than plants (Frampton, van den Brink & Gould 2000). On each sampling occasion, five samples per plot (total  $0.26 \text{ m}^2$ ) were collected and the catch was transferred *in situ* to vials containing *c.* 70% methylated spirit as a preservative. Sampling was carried out only when the crop and soil were dry to touch, and was completed on each occasion within 3.5 h. Arthropods were subsequently separated from soil and plant material in the samples by sieving (minimum mesh

$100 \mu\text{m}$  to ensure retention of small instars). All arthropods except Acari were removed from the samples and adult specimens were identified and counted. Immature specimens of some taxa were also counted (Table 1). Specimens were identified to lower taxa (species, genus or family) where possible using, *inter alia*, the following keys: Fjellberg (1980) and Christiansen & Bellinger (1998) for Collembola; Roberts (1985) for Araneae; Tottenham (1954), Lindroth (1974), Unwin (1988) and several keys by Lohse (see Barnard 1999) for Coleoptera; Oldroyd (1970) and Unwin (1981) for Diptera; Dolling (1991) for Hemiptera; and Goulet & Huber (1993) for Hymenoptera. For the purpose of multivariate analyses, arthropods were assigned to 26 taxa and to four trophic groups (Table 1). A detailed analysis of the response of the collembolan community to the precipitation treatments is reported separately (Frampton, van den Brink & Gould 2000).

#### FUNCTIONAL GROUPS

To test whether the effects of the spring precipitation treatments varied among trophic functional groups, arthropods were classed as herbivores, predators, mycophages or omnivores prior to analysis (Table 1). Polytrophic species and all other taxa that could not be unequivocally classed as herbivores, predators or mycophages were assigned to the omnivore class. Exceptions were that predation among Thysanoptera (Milne & Walter 1997) and polyphagy among predaceous species of Coccinellidae (Majerus 1994; Triltsch 1997) were assumed unimportant (Table 1). In terms of feeding guild, Collembola are usually regarded as generalists but the ecology of many species is poorly known (Rusek 1998). Facultative mycophagy is a widespread trait among Collembola (Hopkin 1997) that would be under-represented if all Collembola were classed as omnivores, so for purposes of trophic analysis the collembolan abundance data were divided equally among mycophages and omnivores (Table 1).

#### ENVIRONMENTAL VARIABLES

Precipitation totals (rainfall and irrigation) received by each experimental plot were recorded daily. Crop growth stage and mean crop height were determined, respectively, on six and seven sampling dates from a random sample of 20 pea plants per plot. Vegetation ground cover was estimated on nine dates using five randomly placed  $50 \times 50$ -cm quadrats per plot. Two randomly placed soil samples per plot of diameter 4 cm and depth 5 cm were collected on each of 12 dates for determining soil moisture content. Maximum and minimum screen air temperatures at the soil surface were measured on five dates using calibrated thermometers placed 1 cm above the soil surface and shielded from direct inso-

**Table 1.** Arthropod taxa and trophic classification used in multivariate analyses of the community response to manipulation of spring precipitation

Taxon	Cohort analysed	Trophic group(s) assigned to taxon
Araneae	All instars together	Predator
Coleoptera:		
Anthicidae	Adults only	Omnivore
Carabidae	Adults and larvae separately	Predator†
Chrysomelidae	Adults and larvae separately	Herbivore
Cryptophagidae	Adults only	Omnivore
Coccinellidae	Adults and larvae separately	Predator‡
Curculionidae	Adults only	Herbivore
Lathridiidae	Adults and larvae separately	Mycophage
Nitidulidae	Adults only	Herbivore†
Phalacridae	Adults only	Mycophage
<i>Tachyporus</i> spp. (Staphylinidae)	Adults and larvae separately	Omnivore
Other Staphylinidae	Adults only	Omnivore, predator*
Other Coleoptera	Adults only	Omnivore†
Collembola	All instars together	Mycophage, omnivore‡
Diplura	All instars together	Omnivore
Diptera:		
Cecidomyiidae	Adults only	Omnivore
Other Diptera	Adults only	Herbivore, predator, Omnivore, mycophage*
Hemiptera:		
Aphididae	All instars together	Herbivore
Other Homoptera	All instars together	Herbivore
Miridae	All instars together	Herbivore†
Other Heteroptera	All instars together	Herbivore, predator*
Hymenoptera:		
Mymaridae	Adults only	Predator
Other Parasitica	Adults only	Predator
Neuroptera	Larvae only (adults absent)	Predator
Symphyla	All instars together	Omnivore
Thysanoptera	All instars together	Herbivore‡

\*Lower taxa (e.g. species, genera) were assigned to different trophic groups.

†Polytrophic taxon represented in samples by only one trophic group.

‡Simplified trophic classification assumed here for brevity (see text).

lation by inverted white plastic tubs (14 × 17 cm; 8 cm high) with perforated sides to permit air circulation.

#### STATISTICAL ANALYSIS

The main dimensions of variation in the species' abundance data were investigated using PCA. A least-squares algorithm in PCA minimizes the total sum of squares in the overall species' data set when the data are regressed against theoretical variables (principal components). The first two principal components were plotted as ordination axes to display the variation among species and samples. Prior to analysis, the species counts were  $\ln(x+1)$ -transformed to normalize the distribution (Jongman, ter Braak & van Tongeren 1995), and the mean of the 20 transformed counts per treatment (four replicates × five samples) obtained. PCA was carried out on the replicate means of transformed data to exclude the variation between replicates, using the software program CANOCO 4 (ter Braak & Šmilauer 1998). Scaling focused on intersample distances, giv-

ing an ordination based on the covariance matrix. Five measured environmental variables were included in the ordination to permit *post hoc* interpretation of the extracted axes. These were: (i) accumulated total rainfall measured during the study; (ii) total rainfall falling in the week (7 days) preceding the sampling date; (iii) soil moisture; (iv) ground vegetation cover; and (v) crop height.

Temporal changes in the effects of the experimental precipitation treatments on the arthropod community were investigated using PRC analysis. This relatively new technique was developed in aquatic ecotoxicology to improve interpretation of temporal changes in the effects of experimental treatments at the community level; these can be difficult to follow in a conventional ordination diagram, particularly if time is not displayed in a single direction (van den Brink & ter Braak 1998, 1999). PRC is a derivative of redundancy analysis (RDA), which is the constrained form of PCA (Jongman, ter Braak & van Tongeren 1995). Whereas PCA displays the contribution of species and samples to all variance in the data set, RDA and PRC focus only on that part of

the total variance which is explained by specified variables (in the case of PRC, on treatment and time). For a set of species  $k$ , treatments  $d$ , and sampling times  $t$ , 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.  $T_{dtk} = b_k \times c_{dt}$  (van den Brink & ter Braak 1998, 1999). The model fitted is:

$$Y_{d(j)tk} = Y_{0rk} + b_k c_{dt} + \epsilon_{d(j)tk} \quad \text{eqn 1}$$

where  $Y_{d(j)tk}$  is the abundance of species  $k$  in replicate plot  $j$  of treatment  $d$  at time  $t$ ,  $Y_{0rk}$  is the mean abundance of species  $k$  in week  $t$  in the control (in our case reference rainfall) treatment ( $d_0$ ),  $c_{dt}$  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  $\epsilon_{d(j)tk}$  is an error term with mean zero and variance  $\hat{\sigma}_k^2$ . 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 & Tso 1982; ter Braak & Looman 1984). By plotting the values of  $c_{dt}$  for each treatment ( $d$ ) and sampling date ( $t$ ), a set of curves (PRC diagram) may be obtained that can be interpreted as the principal response of the community to the experimental treatments. By definition,  $c_{0t} = 0$  for every  $t$ , so the response curve for the reference rainfall treatment is a straight horizontal line against which the fitted curves for drought and irrigation can be contrasted to display clearly temporal changes in treatment effects.

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 compared with the control (reference rainfall) treatment:

$$\exp(b_k \times c_{dt}) \quad \text{eqn 2}$$

which gives the fitted difference in abundance of species  $k$  under treatment  $d$  at time  $t$  relative to the 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 & Šmilauer 1998; van den Brink & ter Braak 1999) (see the Results for an example). Values of  $c_{dt}$  and  $b_k$  were obtained by performing PRC analyses with CANOCO 4 (ter Braak & Šmilauer 1998), both for individual arthropod taxa and for functional groups. Each analysis used the mean per plot ( $n = 5$ ) of  $\ln(x + 1)$ -transformed abundance data (hence four replicate plots per treatment).

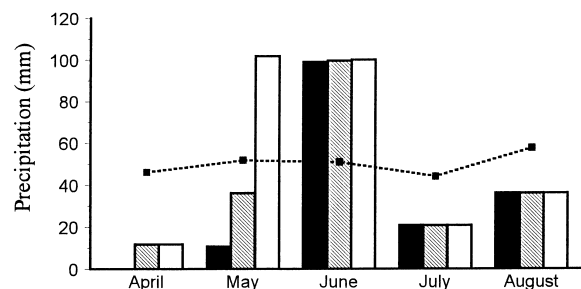
The null hypothesis that the PRC diagram does not display the treatment variance (i.e.  $T_{dtk} = 0$  for all  $d$ ,  $t$  and  $k$ ) was tested using an  $F$ -type statistic

obtained from Monte Carlo permutations of whole time series in the partial RDA from which the PRC was obtained (ter Braak & Šmilauer 1998). Permutation tests of treatments and replicates were also performed separately within each sampling date to test the null hypothesis that on each date  $c_{dt}$  did not differ between treatments. The test of significance of the PRC diagram was performed using 9999 permutations (maximum test resolution  $P < 0.001$ ) whereas 70 permutation options were available for each within-date test (maximum resolution  $P = 0.014$ ). More information on the permutation tests is given by ter Braak & Šmilauer (1998) and van den Brink & ter Braak (1999).

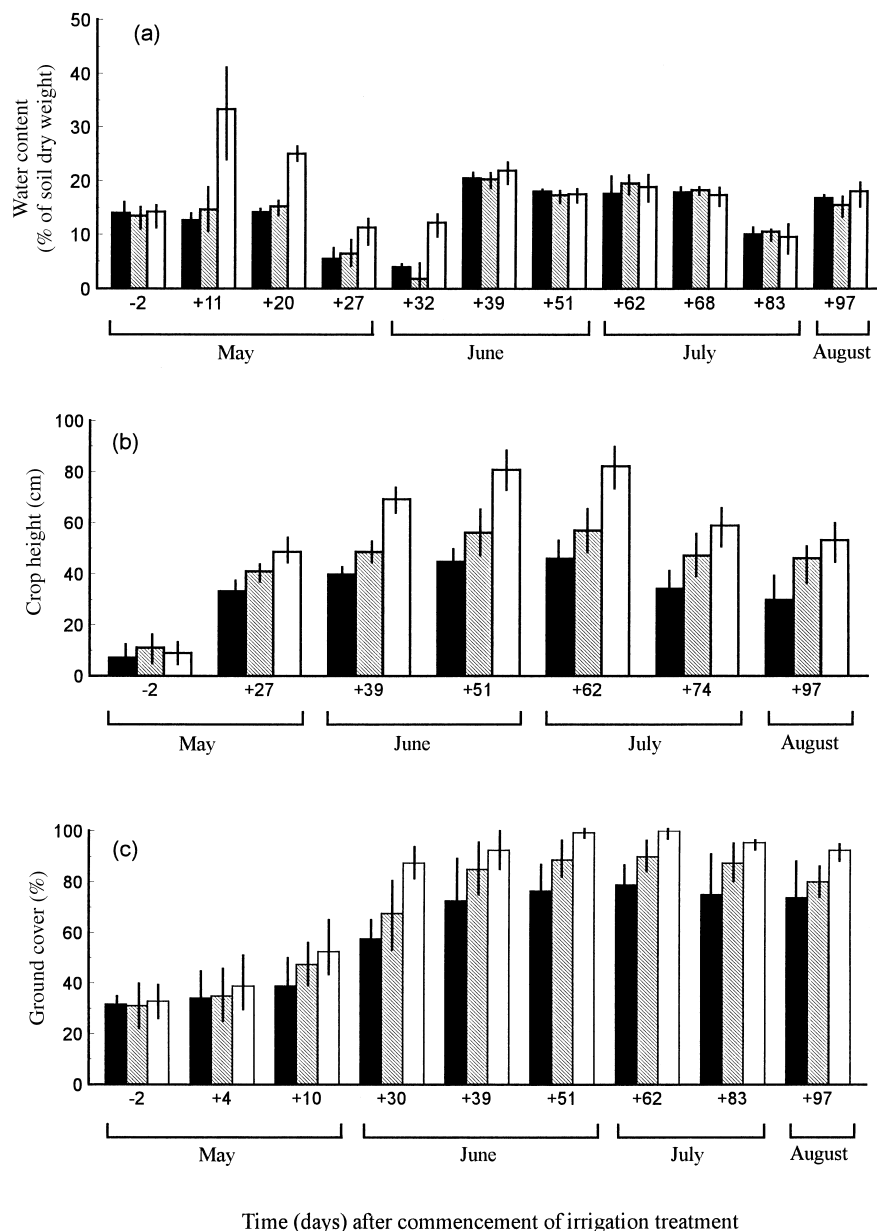
## Results

### ENVIRONMENTAL VARIABLES

Rainfall at the study site was below the long-term average in all months except June (Fig. 2). The largest differences in the quantity of precipitation received by the experimental treatments were in May, after which all treatments received nearly identical amounts; in June this was twice the expected monthly total (Fig. 2). Soil moisture content differed between the experimental treatments only during May and early June, when irrigated plots had a higher moisture content than the other treatments (Fig. 3a). From late May to August, crop height and ground cover were lowest in drought plots and highest under irrigation (Fig. 3b,c). Crop development (indicated by the proportion of plants in different decimal growth stage classes) differed between experimental treatments during June and July (days +39 to +60 relative to the start of irrigation), being most advanced under the drought treatment and least advanced under irrigation. The diel range of air temperatures measured at ground level during July and August (days +71 to +97) was smallest in the irrigated plots; daily maxima were 0.5–3.5 °C



**Fig. 2.** Total precipitation per month received during 1997 by plots under reference (actual) rainfall (shaded bars), spring drought (black bars) and spring irrigation (white bars), and the 20-year (1976–96) site mean monthly total (dashed line).



**Fig. 3.** Mean ( $\pm$  95% CL) soil and vegetation parameters in spring peas during 1997 under reference (actual) rainfall (shaded bars), spring drought (black bars) and spring irrigation (white bars). (a) Soil moisture; (b) crop height; (c) arcsine-dettransformed percentage ground cover. For each variable the mean given is the average of four plot means.

(mean  $2.1^{\circ}\text{C}$ ) lower under irrigation than reference rainfall, whereas daily minima were  $0.1\text{--}3.0^{\circ}\text{C}$  (mean  $1.1^{\circ}\text{C}$ ) higher (Frampton, van den Brink & Gould 2000).

#### ARTHROPODS

Following the application of experimental treatments, counts of all taxa were highest under irrigation and, in most cases, lowest under the drought treatment (Fig. 4). During June to August, approximately twice as many taxa were found in samples obtained from irrigated plots than from drought

plots (Fig. 4p). The abundance of predators, herbivores, omnivores and mycophages was consistently highest under irrigation (Fig. 5); the abundance of herbivores and omnivores differed between all three treatments during June and July, being lowest in drought plots (Fig. 5b,c). Differences in mean counts between the precipitation treatments, as indicated by 95% confidence limits (CL) (i.e.  $P < 0.05$  for non-overlapping CL bars), were occasionally significant for contrasts between drought and reference, but were more consistently significant for contrasts between irrigation and reference (Figs 4 and 5). To obtain an indication of the variation associated with

blocks (i.e. replicates; Fig. 1) in the experimental design, one-way analysis of variance (treatment fixed, block random) was performed on  $\ln(x+1)$ -normalized counts of herbivores at day +52, when treatment differences were large (Fig. 5b). The effect of precipitation treatment was significant ( $F=47.2$ ;  $P < 0.001$ ), but not that of blocks ( $F=0.2$ ;  $P > 0.05$ ) nor the treatment  $\times$  block interaction ( $F=1.1$ ;  $P > 0.05$ ).

#### MULTIVARIATE ANALYSES

The PCA ordination (Fig. 6) displayed 74% of the total variation in the species' abundance data, 59% being explained by the first axis and 15% by the second. Environmental variables explained 58% of the total variance, of which 85% is displayed in the diagram. The spatial pattern of species and samples in the ordination can be interpreted quantitatively using the biplot rule (Jongman, ter Braak & van Tongeren 1995). Most species' points had positive scores on the first axis (Fig. 6). Samples with positive scores on the first axis had higher abundance than the average for the study, and those with negative scores lower than average abundance. During the study arthropod abundance increased under all treatments, the increase being most pronounced under irrigation and least under drought. The greatest abundance of most taxa was recorded under the irrigation treatment between days +32 and +97 (cf. Fig. 4). Differences in species' abundance between the experimental treatments after day +52 are clearly evident in the ordination diagram, where the time trajectories of samples within each treatment after day +52 are indicated by dashed lines. With respect to the second axis, taxa with negative scores had peak abundance earlier in the season (days +32 to +68) than those with positive scores (cf. Figs 4 and 6). The first axis primarily represents the increase in arthropod abundance following colonization of the field by rapidly dispersing migratory species, and the second axis represents a change in the community composition reflecting differences in the temporal dynamics of individual taxa (see the Discussion). In addition to summarizing effectively the abundance data for all individual taxa (Fig. 4a–o), the PCA ordination shows that accumulated rainfall, ground cover and crop height were positively correlated with arthropod abundance in the irrigation treatment; sample coefficients from the PCA correlation matrix for the first axis were, respectively, 0.66, 0.74 and 0.76.

PCA showed the existence of treatment effects, but temporal changes were difficult to visualize in the ordination biplot (Fig. 6). The PRC diagram more clearly indicated the temporal course of treatment effects on the overall arthropod community (Fig. 7). With the analysis upon individual taxa, sampling date accounted for 45% of the total var-

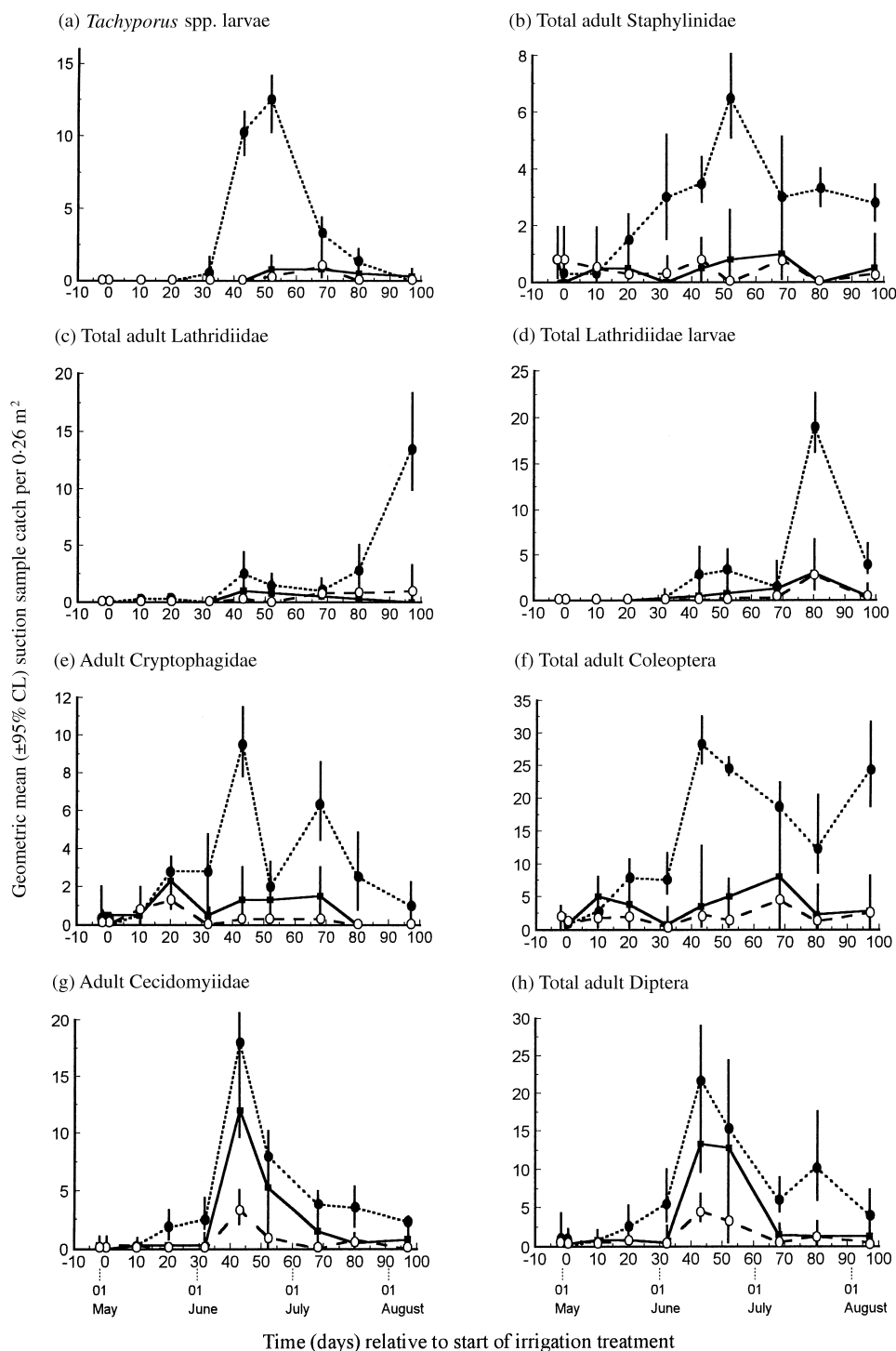
iance of the data set, and treatment 33%, the PRC diagram displaying a significant proportion of the total variance (67%;  $F=59$ ;  $P < 0.001$ ). All taxa had positive species weights, indicating a positive relationship with the treatment effects shown by the PRC diagram; none was obviously favoured by the drought treatment. For taxa with relatively low sampling error there was good agreement between the fitted relative abundance obtained from the PRC analysis and that observed in the original data. For example, the fitted relative abundance of Collembola under irrigation at day +43, as obtained from the species' weights ( $b_k$ ) and principal response ( $c_{di}$ ) (equation 2), was  $\exp(1.83 \times 0.81) = 4.4$  (Fig. 7); this is precisely the ratio of the actual mean abundance under irrigation to that under reference rainfall on day +43 (Fig. 4o). For most taxa, however, a discrepancy between fitted and actual values of relative abundance reflected heterogeneity of the original counts (as indicated by confidence limits for the mean data in Figs 4 and 5). Effects of irrigation were statistically significant on more occasions than those of drought (Fig. 7) and persisted to the end of the study (+97 days after irrigation commenced).

An almost identical PRC diagram (not illustrated) was obtained when data were analysed as trophic functional groups. The diagram accounted for a significant proportion of the treatment variance (92%;  $F=146$ ;  $P < 0.001$ ). Of the total variance, 61% was explained by sampling date and 27% by treatment. Species' weights were very similar for predators, mycophages and omnivores (range 1.01–1.05) and slightly lower for herbivores (0.88). The functional groups thus responded similarly to the precipitation treatments. Mycophages and omnivores comprised equal numbers of Collembola, which dominated the catch, accounting for their almost identical response in PRC analysis. It is unlikely that exclusion of Collembola from the analysis would have made much difference to PRC results because trophic groups responded similarly to the precipitation treatments when Collembola were not included (Fig. 5). Permutation testing of the treatment effects per sampling date using trophic group yielded the same pattern of statistically significant treatment differences as the analysis by individual taxa, except for the comparison between drought and reference treatments for which treatment effects were significant only at three sampling dates ( $P < 0.05$ ; days +10, +32 and +52) (cf. Fig. 7).

#### Discussion

##### RELEVANCE OF THE PRECIPITATION TREATMENTS

The treatments were intended to mimic quantities of precipitation that would be realistic in terms of their likelihood of occurrence, either as meteorological



**Fig. 4.** (a–o) Geometric mean suction catch per plot ( $\pm 95\%$  CL;  $n = 4$ ) of 15 arthropod taxa; (p) mean number of arthropod taxa per plot ( $n = 4$ ) under reference (actual) rainfall (squares), spring drought (white circles) and spring irrigation (black circles). Data are from five pooled samples per plot (total 0.26 m<sup>2</sup>). Note different ranges of the axes.

events (drought, rainfall) or agricultural activity (irrigation). The 58-day spring drought treatment would equate to a severe drought in southern England (Marsh 1996) while the irrigation treatment mimicked possible scenarios of heavy rain or crop irrigation (details below). Spring 1997 was drier

than usual in southern England (with 40 consecutive dry days at the study site), and consequently the reference rainfall treatment received *c.* 16 mm (30%) less rainfall during May than the 20-year site average. Use of the reference treatment as a yardstick against which to judge the effects of drought and



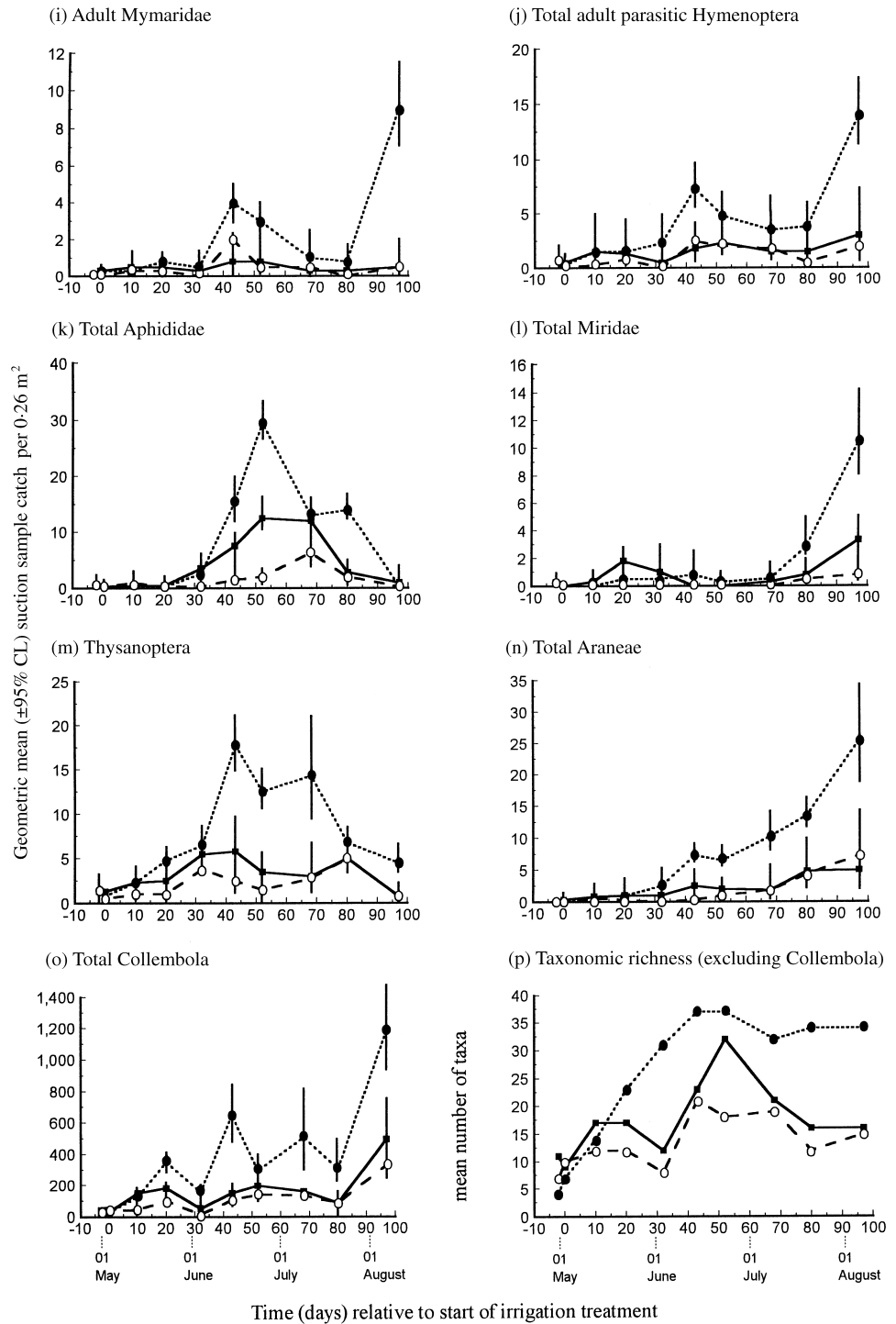
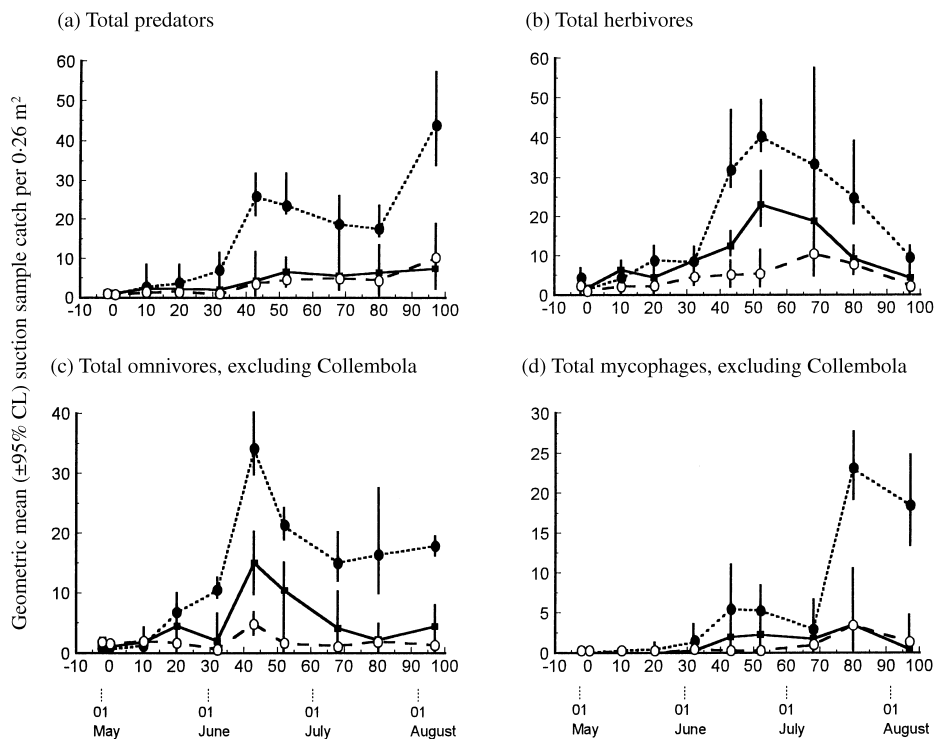


Fig. 4 (continued)

irrigation could thus underestimate the impact of drought, and exaggerate that of irrigation relative to conditions that would be more 'typical' of spring precipitation. Nevertheless, our results indicate the potential importance for farmland arthropods of short-lived weather events in spring, and illustrate the range of variation in abundance that extremes of spring rainfall may cause.

#### COMPARISON WITH RAINFALL DATA

Weather records for the study site (1976–96) indicate that rainfall of an equivalent intensity to the maximum rate of irrigation used in our study (40 mm 24 h<sup>-1</sup> in May) occurred once in 20 years. The only comprehensive records to resolve rainfall distribution to 1-h periods (UK Meteorological Office,



**Fig. 5.** Geometric mean suction catch per plot ( $\pm 95\%$  CL;  $n = 4$ ) of four trophic groups under reference (actual) rainfall (squares), spring drought (white circles) and spring irrigation (black circles). Data are from five pooled samples per plot (total  $0.26 \text{ m}^2$ ). Note different ranges of the axes.

unpublished data) give a 100-year return time for  $40 \text{ mm h}^{-1}$  rainfall at any one site, but this would overestimate the return time for southern England as a whole; overestimation is also likely because historical records often do not take recent climate change into account (Marsh 1996). The monthly total (rainfall + irrigation) received by irrigated plots during May 1997 (98 mm) was exceeded at the study site by natural precipitation on two occasions during 1976–96. The irrigation treatment would thus represent heavy rainfall in May of an intensity that, though infrequent in occurrence, is not without precedent.

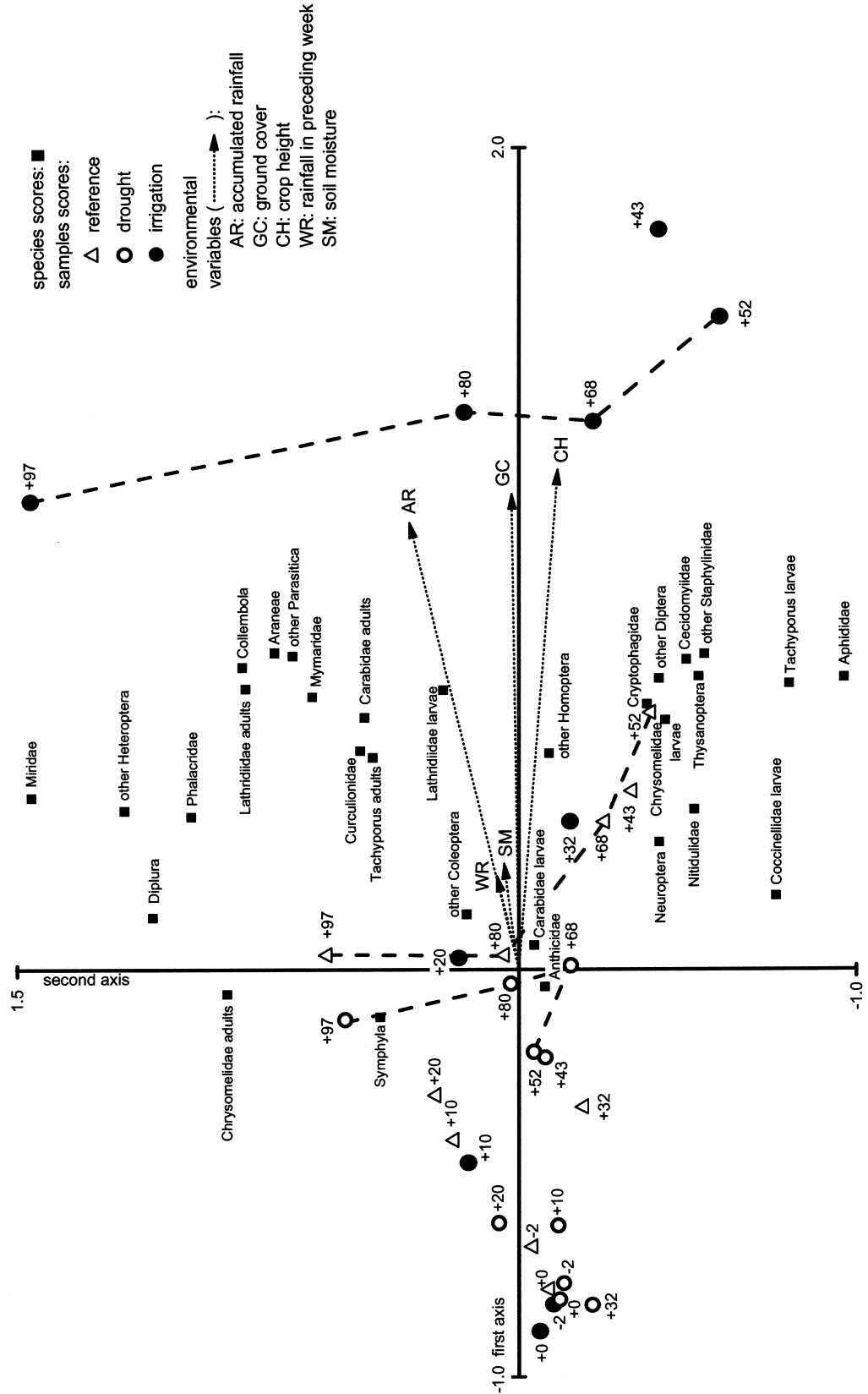
#### COMPARISON WITH IRRIGATION PRACTICE

Irrigation practice in British arable crops varies with soil type, crop, growth stage and weather, but a typical figure would be *c.* 25 mm applied in 30–45 min, repeated at intervals of several days (ADAS, unpublished data; MAFF 1982). Irrigation on 2 May slightly exceeded the typical hourly rate practised by most growers (except those without a restricted irrigation supply or the need to protect higher-value crops; Bailey 1998), but was realistic in the quantity that would be applied per week. Irrigation of peas in Britain is of relatively minor importance compared with potatoes and sugar beet (Stansfield 1997), but the findings of our work are

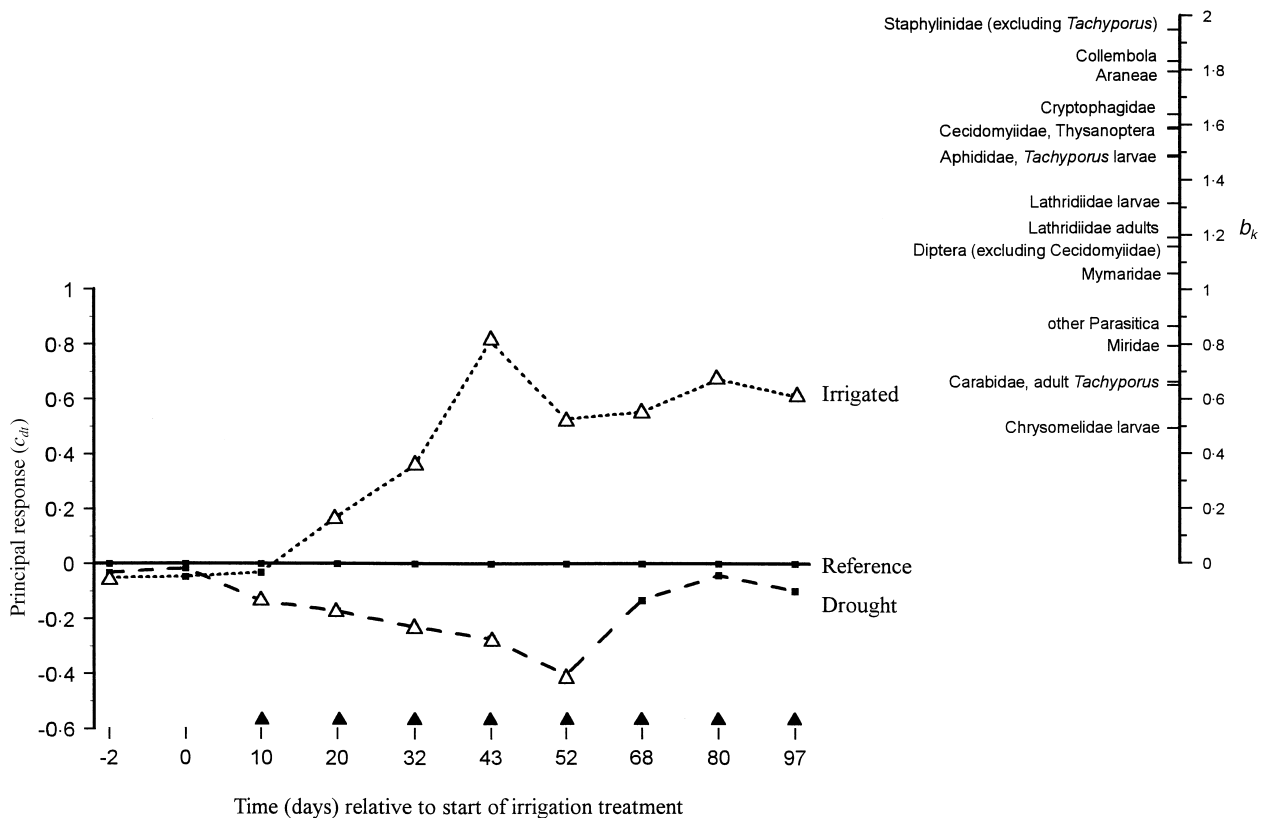
relevant to these crops for two reasons: (i) many of the arthropod taxa encountered in the present work occur widely in arable land and are not crop-specific; (ii) foliage development of any spring-sown crop planted under dry conditions would be expected to benefit from early irrigation. In this respect, our results would be expected to differ from those obtained in an autumn-sown crop irrigated during a period of spring drought, or a spring-sown crop irrigated during summer (Bailey 1998). The fact that a short period of irrigation led to persistent effects on vegetation and arthropods suggests that irrigation has potential as a tool for managing vegetation and arthropod abundance, e.g. to enhance natural enemy abundance or improve food availability for insectivorous wildlife (see below). This is not a prospect, however, as current limitations on the availability of irrigation water are unlikely to improve (Jaggard, Dewar & Pidgeon 1998).

#### SAMPLING CONSIDERATIONS

Suction sampling captures predominantly surface-active species so our findings refer only to the above-ground cohort of the arthropod community. This is an ecologically important component of the fauna, comprising crop pests and their natural enemies, and species important as a food resource for



**Fig. 6.** PCA ordination diagram (covariance biplot) of species' abundance data from three precipitation treatments and with five measured environmental variables. Numbers indicate the sampling date (days relevant to the start of the irrigation treatment). Axis scaling is for sample scores. One unit is equivalent to 2.0 for environmental variables and 4.0 for species' scores. Dashed lines show the time-course of each treatment from day +52.



**Fig. 7.** PRC diagram and species' weights ( $b_k$ ) showing the overall impact on the arthropod community of spring drought (dashed line) and spring irrigation (dotted line) relative to reference (actual) rainfall (solid line). Triangles denote values of  $c_{dt}$  that differ significantly ( $P < 0.05$ ) from the reference rainfall treatment (white triangles) or between drought and irrigation treatments (black triangles).

farmland wildlife. Suction sampling has been used in other studies to investigate arthropod abundance on farmland (Vickerman 1992; Ewald & Aebischer 1999) but catches can be biased by effects of vegetation density on sampling efficiency. Samples in our study were taken between crop plants to avoid this problem. Care was also taken to ensure that understorey vegetation would not have influenced sampling efficiency, and there was no evidence that sampling efficiency was affected by differences between treatments in soil moisture (Frampton, van den Brink & Gould 2000). Catches mainly reflected the density of arthropods on the ground surface, but would have included plant-dwelling species that had fallen from plants (Winder 1990) and species dispersing on the ground.

#### TEMPORAL PATTERNS IN ABUNDANCE

The composition of the arthropod community changed during the summer, reflecting differences in the temporal dynamics of individual taxa. Abundance tended either to peak during June and July, followed by a decline (e.g. Aphididae, Staphylinidae, Thysa-

noptera), or to increase to reach a peak at the end of the study in August (e.g. Araneae, Hymenoptera, Lathridiidae). Among Carabidae, Chrysomelidae, Lathridiidae and *Tachyporus* spp., peak abundance of larval instars clearly preceded a later peak in the adult cohort. The temporal patterns displayed by PCA are broadly as would be expected for the epigeic arthropod community of a temperate spring-sown arable crop. Low initial abundance of most taxa during early crop development is consistent with negative effects of cultivation prior to sowing (Stinner, Krueger & McCartney 1986) and may also reflect an effect of the plot barriers impeding colonization by arthropods walking on the ground. Barriers were employed to minimize possible heterogeneity in arthropod distribution associated with dispersal from the hedgerow in spring (Coombes & Sotherton 1986) but it is unlikely that they would have compromised the realism of the study as arable fields vary considerably in their margin types, not all of which are good sources of arthropod immigrants. A synthetic pyrethroid insecticide sprayed on 1 May against *Sitona* spp. (Curculionidae) could also have contributed to the low

initial abundance of several arthropod groups (Theiling & Croft 1988) but probably would not have adversely affected Collembola (Frampton 1999). This insecticide, and also the herbicides sprayed on 15 May, were applied to all experimental plots as conventional crop management practice and are an integral part of the study in terms of its realism.

Numbers of aphids and other crop-feeding herbivores (e.g. Cecidomyiidae, and Thysanoptera) increased in spring when plant nutrient quality and temperature would have been optimal for growth and reproduction (Dixon 1989), while other herbivores (e.g. Chrysomelidae and Curculionidae) exhibited later peaks in abundance and included species associated with weeds, together with small numbers of *Sitona* spp. which had recolonized the pea crop. Aphid-specific predators such as Coccinellidae and a number of polyphagous Carabidae and Staphylinidae invade fields during spring (Coombes & Sotherton 1986), where they feed upon aphids and other animal, plant and fungal material (Sunderland 1975; Wratten & Powell 1991), reproduce, then disperse in late summer to overwintering sites outside the crop (Petersen 1998). Carabidae were poorly represented in our study, probably because only small species are captured by suction sampling and the plot barriers may have impeded dispersal of some flightless species from the hedgerow. The increase in abundance of Araneae (which were mostly Linyphiidae) during July and August most probably reflects emigration dispersal (Thomas & Jepson 1999). There was also a general increase in the abundance of Collembola during the summer, but the two orders responded differently, with species of Symphypleona exhibiting an earlier peak in abundance than those of Arthropleona (Frampton, van den Brink & Gould 2000).

An obvious limitation of our study is that it was conducted in only one year and therefore could not fully investigate the persistence of effects of spring precipitation. As many of the arthropod taxa whose abundance was affected by the precipitation treatments during June would have emigrated from the arable field before harvest, possible effects of the treatments on their overwintering populations and the implications for subsequent colonization of arable fields the following spring remain unknown. Effects of the precipitation treatments on abundance were clearly evident among those arthropods that remained in the field up to harvest, which raises the question of whether the effects would have persisted beyond harvest if the field had remained under stubble. The possible implications for insectivorous wildlife feeding in stubble fields during autumn and winter warrant consideration in this context.

## EFFECTS OF THE SPRING PRECIPITATION TREATMENTS

Spring drought had an overall negative impact on arthropod abundance, while that of irrigation was positive. Relative to reference rainfall, effects of the irrigation treatment were larger than those of spring drought. This pattern is consistent with the distribution of precipitation among treatments during May, when the difference between irrigated and reference plots (c. 65 mm) exceeded that between drought and reference (c. 25 mm).

## IMPACT ON POTENTIAL PESTS

Changes in the trophic structure of the arable arthropod community would be a cause for concern if patterns of precipitation were to favour pest species relative to their natural enemies (Cammell & Knight 1992) or stimulate emergence of secondary pests. Some of the Collembola species we sampled are agricultural pests in drier climates, where outbreaks may be triggered by rainfall following drought, raising the possibility that changing patterns of precipitation could promote such species as pests in northern Europe (Frampton, van den Brink & Gould 2000). Epigeic Collembola did not appear to pose any threat to the crop following any of our manipulations of precipitation, however, as very few were found on the pea plants after flowering. Despite the potential for drought to influence positively populations of certain arthropods (Mattson & Haack 1987), we found no evidence for a favourable effect of the spring drought treatment on any of the sampled taxa; the highest abundance of nearly all taxa and functional groups occurred under the spring irrigation treatment. Irrigation did increase the abundance of potential pests of the pea crop (Aphididae and Curculionidae) relative to the other treatments, but natural enemy abundance (e.g. of Carabidae, Staphylinidae and Araneae) also increased. Following our manipulations of precipitation, abundance of aphids and *Sitona* spp. did not exceed treatment thresholds and no arthropod pest control measures were required.

## MECHANISMS OF TREATMENT EFFECTS

Vegetation structural complexity, including vegetation height and ground cover which differed between the precipitation treatments, is an important determinant of arthropod abundance and diversity in agroecosystems. Increases in vegetation structural complexity and ground cover are usually associated with increases in abundance and diversity of arthropods, e.g. as a result of effects on food availability and microclimate (Honek 1988; Lagerlöf & Wallin 1993; Lys, Zimmerman & Nentwig 1994; White & Hassall 1994; Frank & Nentwig 1995; Hawthorne &

Hassall 1995; Costello & Daane 1998; Petersen 1998; Kromp 1999; Thomas & Marshall 1999). A plausible mechanism for the observed effects would be that spring precipitation caused changes in vegetation which in turn influenced arthropod abundance and species composition (McPherson *et al.* 1998). Potentially complex vegetation-mediated effects of precipitation are possible, as a plant's response to water stress can influence herbivore population dynamics through changes in nutrient status and physiology (Mattson & Haack 1987; Masters *et al.* 1998; Fox *et al.* 1999) with implications for multitrophic arthropod-plant interactions (Price *et al.* 1980; Masters, Brown & Gange 1993; Gange & Brown 1997). An example of the complexity of plant-mediated indirect effects of precipitation on arthropods is the variation in the performance of aphids on drought-stressed relative to healthy plants, which may be increased, decreased or unchanged depending upon the aphid species, host-plant, timing and severity of the stress (Pons & Tatchell 1995).

Spring precipitation clearly had an impact on microclimate at the soil surface, as both diel temperature range and soil moisture differed between the precipitation treatments. The differences in soil moisture reflect measurements made in the top 5 cm of soil. Shallow samples were taken so as to be relevant to epigeic species, as strong evaporation in summer (Marsh 1996) would influence the moisture content of surface soil. Differences between treatments in moisture near the soil surface could explain the observed responses of taxa whose development is critically dependent upon optimal conditions of soil moisture, e.g. Collembola (Fig. 4o) (Ashraf 1971) and *Tachyporus* larvae (Fig. 4a) (Petersen 1998). Soil moisture can also influence communities of soil bacteria and fungi (Schnürer, Clarholm & Rosswall 1986; Whitford 1992), and hence, indirectly, mycophagous and detritivorous species. It is also possible that some arthropod taxa may have migrated vertically in the soil profile in response to the changes in microclimate (Frampton, van den Brink & Gould 2000). While our data do not prove any of the above causal mechanisms, the persistence of the effects on the arthropod community, together with the time lag that followed irrigation before the abundance of some taxa increased, indicates that the effects of spring precipitation on the arthropod community were probably mainly indirect. Whatever the causal mechanisms, the fact that both vegetation growth and arthropod abundance were affected for several months by spring precipitation has implications for the conservation of farmland wildlife (considered below).

PRC analysis is a relatively new method, developed originally to aid impact assessments of pollutant stress on aquatic biological communities in mesocosms. The fact that it has previously been applied only in aquatic ecotoxicology (van den Brink & ter Braak 1997, 1998, 1999; Kedwards, Maund & Chapman 1999) reflects a greater emphasis on community-level studies in aquatic than terrestrial ecotoxicology. The PRC method is relevant to any synecological study investigating temporal changes in community composition in response to experimental treatments, but for valid statistical interpretation of treatment contrasts a PRC diagram must be based on a replicated-design study. PRC diagrams may be used to display long-term changes in community composition in monitoring studies where replication is not feasible, provided that adequate care is taken with the experimental design and interpretation to avoid pseudoreplication (Frampton 2000). At least five treatment levels may be displayed in a PRC diagram without loss of visual clarity (van den Brink *et al.* 2000).

In our case (as in other studies; van den Brink & ter Braak 1997, 1998, 1999) the PRC diagram has a distinct advantage over the ordination diagram because it clearly displays the temporal changes in the magnitude of treatment effects and allows the start and end points of effects to be determined (e.g. based upon the statistical significance of differences from the reference treatment; van den Brink & ter Braak 1999). By conducting 30 permutation tests (three treatment comparisons  $\times$  10 sampling dates), each with a type I error rate of 5%, we accept that two of the significant effects displayed in the PRC diagram could have been achieved purely by chance. This does not affect substantially our interpretation of treatment effects as we make no attempt to draw conclusions from the outcome of individual tests (in cases where interpretation at the level of individual tests is required, the experiment-wise error rate could be adjusted to limit type I errors; Sokal & Rohlf 1995). The consistency of differences between treatments ( $c_{dt}$  values consistently positive for irrigation and consistently negative for drought), coupled with the overall number and distribution of significant differences, give clear evidence for the persistence of treatment effects. The patterns displayed in the PRC diagram suggest that recovery of the community after drought occurred sooner than recovery after irrigation. This information, which cannot be obtained directly from the PCA ordination, is consistent with differences in the amount of precipitation the treatments received (see above). The visual clarity of the PRC diagram and its relative simplicity of interpretation make it a potentially effective

means of presenting complex ecological information in a format accessible to non-experts.

Species' weights indicate how likely each taxon is to follow the fitted response for the whole community as displayed in a PRC diagram. A positive weight indicates a response pattern consistent with that displayed in the diagram for the overall community, and a negative weight indicates an opposite response. PRC diagrams can thus provide a useful insight into ecological interactions by identifying taxa with opposite responses to a given treatment (van den Brink *et al.* 2000). We omitted taxa with weights between  $-0.5$  and  $+0.5$  because they are likely to show either a weak response or one that is unrelated to that indicated in the PRC diagram (van den Brink & ter Braak 1999). A taxon that is numerically important could in theory have a low species' weight if its response pattern is unrelated to that displayed by PRC analysis (van den Brink & ter Braak 1999), but such a situation may be easily identified by checking the counts of taxa with low species' weights; in our case all taxa excluded on the basis of low species' weights were rare in samples.

#### IMPLICATIONS FOR WILDLIFE CONSERVATION

The fact that precipitation during May affected the abundance and taxonomic richness of epigeic arthropods up to harvest in August has implications for the conservation of farmland arthropods under predicted future increases in the frequency and intensity of droughts. It has been argued that insect biodiversity should be preserved to protect ecosystem function (Samways 1994; Hågvar 1998; Altieri 1999), and many farmland arthropods warrant conservation on account of their potential as natural enemies of crop pests (Wratten & Powell 1991; Sunderland *et al.* 1997; Kromp 1999) and as indicators of habitat quality or agricultural management (Kromp 1990; Paoletti & Bressan 1996; van Straalen 1998; Paoletti 1999). They are also important in the diet of insectivorous wildlife, including small mammals (Johnson, Flowerdew & Hare 1992) and birds (Potts 1986; Moreby & Sotherton 1997; Wilson *et al.* 1999; Borg & Toft 2000). Considerable effort has been devoted to investigating the causes of declines in farmland bird populations (Boutin, Freemark & Kirk 1999; Chamberlain *et al.* 1999; Chamberlain, Wilson & Fuller 1999; Pärt & Söderström 1999; Robinson & Sutherland 1999; Siriwardena, Baillie & Wilson 1999; Brickle *et al.* 2000; Chamberlain 2000; Hendersen *et al.* 2000; Siriwardena *et al.* 2000; Storate, Borralho & Araújo 2000), which could include changes in the availability of arthropods (Ewald & Aebischer 1999; Moreby & Southway 1999; Wilson *et al.* 1999). Several arthropod taxa, e.g. Araneae, Coleoptera and Hymenoptera, which are important in the diet of birds, have declined in abundance on

arable farmland (Aebischer 1991; Ewald & Aebischer 1999; Kromp 1999), although the contribution of climatic variation is not certain. Detailed studies of the grey partridge *Perdix perdix* L., whose populations have declined globally (Potts 1986; Bro *et al.* 2000), have shown that chick survival depends upon arthropod availability and that a relatively small decrease in chick survival rate would considerably delay population recovery (Potts 1986). Even infrequent droughts could thus have long-term consequences for farmland bird populations if changes in food availability are sufficient to cause populations to drop below the threshold for short-term recovery. The possible implications of drought for granivorous species also warrant consideration, as our spring precipitation treatments affected the development both of the crop and its weed flora. There is strong circumstantial evidence that drought in North Africa has had a major negative impact on British breeding populations of at least four migratory passerine species, probably as a result of decreased plant and arthropod availability at wintering grounds in the Sahel (Marchant *et al.* 1990).

#### FUTURE PROSPECTS

The persistence of the effects of spring precipitation on farmland arthropods, and the potential implications for insectivorous wildlife, underline the need for a better understanding of how farmland arthropod communities respond to different patterns of precipitation. With changing climate this need will become more urgent. Little work has been done so far to examine the importance of precipitation for farmland arthropod synecology, and future studies will be able to address only a small proportion of precipitation patterns. Research effort must therefore focus on specific weather scenarios deemed likely to have the greatest impact on arthropods, or those likely to provide the most useful comparative data. In this respect, priorities should be to: (i) characterize the arthropod abundance and community composition under 'typical' patterns of rainfall, as a reference against which effects of extreme precipitation events can be quantified; (ii) investigate arthropod responses to anticipated extremes of precipitation (whose occurrence is either predicted by models of climate change or based on recent historical weather records); and (iii) investigate effects of precipitation on farmland arthropod communities in the long term. Strategies for obtaining this information include the analysis of existing farmland arthropod data sets in relation to weather data, simulation modelling to predict responses of arthropods to different rainfall scenarios, and long-term field monitoring studies of the effects of actual and manipulated regimes of rainfall.

A serious impediment to field studies investigating effects of precipitation on arthropods in a temperate

climate is the unpredictability of natural precipitation. Our study was conducted during a period of dry weather because it was easier to manipulate precipitation by watering plots than by shielding them from rainfall; shielding of plots in the arable field was labour intensive and would not have been practical during extended periods of wet weather, for example as occurred in June when rain fell on 13 consecutive days. Use of automated rain shelters (such as those used in the TIGER studies; Masters *et al.* 1998) would have improved control of precipitation but was impractical for a short-term study in an arable field. There is thus a need to establish long-term monitoring and manipulative work on arable farmland that can integrate automated rain shielding of experimental plots with crop management activities (e.g. agrochemical applications and cultivation). Without such an initiative, it is difficult to see how realistic field-based empirical research into effects of precipitation on arable arthropod synecology can progress, given the difficulty of manipulating precipitation in a temperate climate.

### Acknowledgements

We thank Ben Gibbons for permission to conduct this study in a commercial crop on the Leckford Estate, Tom Palmer for providing long-term meteorological records for the study site, Dave Baddams and Nick Smith for help with organizing fieldwork equipment, and Mike Green and Simon Groves (ADAS) for information on irrigation practices. We also thank the editors and two anonymous referees for their valuable comments that enabled us to improve the manuscript.

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Received 24 August 1999; revision received 22 March 2000