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Diel activity patterns in an arable collembolan community

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Abstract

Diel patterns of activity and abundance among soil-surface Collembola in a wheat crop in southern England were investigated in summer using pitfall trapping, suction sampling and sweep-net sampling. The multivariate technique principal response curves (PRC) analysis was used to investigate changes in the overall community composition within and between sampling dates. Catches of Collembola obtained using all three sampling methods were generally highest from 12.00 to 00.00 h and lowest from 00.00 to 06.00 h, but diel patterns varied among species and were more variable for pitfall than suction samples. Pitfall catches of *Lepidocyrtus cyaneus* and also of the total Collembola were correlated positively with soil-surface temperature. The above-ground abundance of Arthropleona estimated by suction sampling varied by ca. 870 m^{-2} in a 24-h period, suggesting that availability of Collembola to predatory arthropods could change considerably in a short time. These findings have implications for arthropod sampling strategies, exposure of Collembola to agrochemicals and predation of Collembola in agroecosystems.

Keywords: Collembola; Sampling method; Temporal dynamics; Activity; Abundance; Principal response curves

1. Introduction

Diel (24 h) activity patterns have been extensively studied for macroarthropods, but comparable information is mostly lacking for Collembola, even though they are among the most abundant of the epigeic arthropods in agroecosystems and are ecologically important in food webs (Rusek, 1998). Diel cycles in collembolan locomotor activity and moulting behaviour have been observed both under controlled laboratory conditions (Cutkomp et al., 1987) and in response to cyclic changes in environmental variables in field studies. The strongest evidence for predictable diel cycles of activity in the field has come mainly from arctic habitats with 24 h daylight in summer (Ruppel, 1968; Mobjerg Kristensen and Vestergaard, 1975; Solem and Sendstad, 1978; Zettel, 1984; Fox and Stroud, 1986) or hot deserts where regular diel changes in water stress occur (Hussein, 1976; Whitford et al., 1981; MacKay et al., 1987). In temperate regions, diel cycles in the activity or vertical migration of Collembola have been observed on tree trunks and shrubs (e.g. Gisin, 1943; Bauer, 1979), in vegetable crops (Davies, 1932) and on a rooftop (Moon and Gough, 1972). These activity patterns have been attributed to changes in humidity and temperature, to which Collembola are very sensitive (e.g. Joosse, 1970; Joosse and Groen, 1970; Bauer, 1979;

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Verhoef and Van Selm, 1983). As collembolan reactions vary interspecifically to humidity (e.g. Davies, 1928), temperature (e.g. Ashraf, 1971) and light (e.g. Bowden et al., 1976; Ponge, 1993; Salmon and Ponge, 1998), diel changes in these factors could influence the collembolan community composition estimated at different times and using different sampling methods. Several workers have investigated diel variation in collembolan locomotor activity in woodlands (Joosse, 1965; Bowden et al., 1976; McBrayer et al., 1977; Brand, 1979), but so far only one detailed study of diel activity among farmland Collembola has been carried out, in a heavily grazed pasture using a time-sorting pitfall trap (Desender et al., 1984).

This paper reports diel patterns of activity and abundance observed in the epigeic collembolan community of a wheat crop in summer, where short-term temporal changes in collembolan activity and abundance could influence exposure to pesticide applications and other diurnal farming activities. The aim was to determine whether significant changes in community composition, estimated using different sampling methods, occur within a 24-h period, and hence whether estimates of abundance and activity based only on diurnal sampling would be biased (Brand, 1979). For analysis of changes in community composition, the relatively new multivariate technique of principal response curves (PRC) analysis was used.

2. Material and methods

2.1. Study site

The analyses reported here were applied to a hitherto unpublished data set (Frampton, 1989) which was obtained from a 7.3 ha field of winter wheat cv. Moulin in southern England (51°8′N, 1°30′W) in summer 1987. The crop was drilled on 31 October 1986 and harvested on 31 August the following year; the field had been under arable cropping for at least 10 years prior to the study. Soil type was a light loam over chalk (Andover series). A 15 m × 15 m sampling area, located 35 m from the nearest hedgerow (mainly *Crataegus monogyna* Jacq.), was established in the field, within which all sampling was carried out to minimise spatial variation in arthropod captures and to ensure that sampling efficiency was not influenced by vegetation density. Several applications of fungicides, herbicides, fertilisers and a growth regulator were made to the wheat crop as routine farming practice, but only fungicides were applied during the period of the Collembola study. Four active ingredients were applied as a tank mix on 16 June, comprising carbendazim (250 g.a.i. ha^{-1}), maneb (1600 g.a.i. ha^{-1}), triadimenol (63 g.a.i. ha^{-1}) and tridemorph (188 g.a.i. ha^{-1}). Of these, triadimenol is toxic to some Collembola in wheat whereas toxicity of carbendazim to Collembola has so far been demonstrated only in the laboratory (Frampton and Wratten, 2000). The possible effect of these fungicides on the diel distribution of Collembola catches is considered when interpreting the results (Section 4.1).

2.2. Sampling methods

Three methods were used for sampling Collembola. The number of samples chosen in each case was a compromise between sampling precision (many samples preferable) and, on the other hand, the risk of depleting the fauna, and the limited availability of resources for sample processing (few samples preferable) (Frampton, 1989). Suction samples were used to estimate collembolan abundance on the soil and vegetation, pitfall traps to provide a measure of activity on the soil surface, and sweep net samples to give an indication of collembolan occurrence on the crop plants (i.e. climbing behaviour).

2.2.1. Suction sampling

A ‘D-vac’ suction sampler (Dietrick Backpack Model 1A; Dietrick et al., 1960), which had a high efficiency of collecting epigeic Collembola from the soil surface in a cereal crop (Frampton, 1989), was used to obtain estimates of collembolan abundance on the soil and plants. Each sample (0.46 m^2) was obtained by pooling the catch from five 0.092 m^2 sub-samples collected by holding the suction nozzle (diameter 0.342 m) on the ground for 10 s at each of five randomly-chosen locations. The sampler contained a muslin net (mesh size < 100 μm) which was sufficiently long to allow crop plants to enter it when the suction nozzle was placed on the ground. On each sampling occasion, five suction samples were obtained from random locations in the study area, avoiding the area within 0.5 m of each pitfall trap (see below).

Table 1
Timing of diel Collembola sampling on each of seven sampling occasions in summer[a]

Sampling date		Sampling time, BST (GMT + 1) (h)			
Occasion	Days	00.00–06.00	06.00–12.00	12.00–18.00	18.00–00.00
1	1 June	D1	D2	D3, P1	D4, P2
	2 June	P3	P4	P5	P6
	3 June	P7	P8		
2	16 June			P1	P2
	17 June	P3	P4	P5	P6
	18 June	P7	P8		
3	29 June			D1, P1, S1	D2, P2, S2
	30 June	D3, P3, S3	D4, P4, S4	P5	P6
	1 July	P7	P8		
4	8 July	D1, S1	D2, P1, S2	D3, P2, S3	D4, P3, S4
	9 July	P4	P5	P6	P7
	10 July	P8			
5	20 July			P1	P2
	21 July	P3	P4	P5	P6
	22 July	P7	P8		
6	27 July			P1	P2
	28 July	P3	P4	P5	P6
	29 July	P7	P8	D1, S1	D2, S2
	30 July	D3, S3	D4, S4		
7	4 August		D1, P1, S1	D2, P2, S2	D3, P3, S3
	5 August	D4, P4, S4	P5	P6	P7
	6 August	P8			

[a] Within each occasion, P1–P8 are eight consecutive 6-h periods of pitfall trapping, D1–D4 are four consecutive suction samplings (five occasions), and S1–S4 are four consecutive sweep net samplings (four occasions). Diel time ranges refer to pitfall sampling and underscored times to suction and sweep sampling. For each sampling occasion, pitfall catches of Collembola from the same catch time on consecutive days were pooled (i.e. P1 + P5, P2 + P6, P3 + P7 and P4 + P8).

Samples were taken only when both the crop and soil were dry, to minimise any influence of surface moisture on sampling efficiency (e.g. captured Collembola adhering to the sampler net). Suction samples were collected at 00.00, 06.00, 12.00 and 18.00 h local time (British Summer Time, BST), on five occasions from June to August (Table 1). This frequency of sampling was considered the maximum that could be accommodated in terms of sample sorting effort and potential disturbance to the study area. For clarity, all times given below refer to BST (GMT + 1 h).

2.2.2. Pitfall traps

Ten pitfall traps (9 cm diameter white plastic beakers) were installed flush with the soil surface; each was supported in a plastic cylinder for ease of removal and replacement and to minimise disturbance to the surrounding soil. The cylinders were installed in the soil at least 1 week before any traps were operated, to reduce any impact of the initial soil disturbance on subsequent trap catches (the ‘digging-in effect’; Joosse and Kapteijn, 1968; Digweed et al., 1995). Two rows, ca. 3 m apart, each comprising five traps at 2 m spacing, were located in the centre of the study area. The regular arrangement of traps was necessary to minimise disturbance to the plot during trap changing and to ensure that suction samples were not taken close to pitfall traps (a small battery-powered torch was the only artificial illumination used to guide sampling under dark conditions). Each trap was 10 cm deep and contained a 3 cm depth of water with a drop of detergent to break the surface tension so that captured arthropods were drowned to avoid escape, dehydration or predation. Preliminary sampling with traps set for four consecutive 6-h periods (00.00–06.00, 06.00–12.00, 12.00–18.00 and 18.00–00.00 h) on 1–2 June yielded low catches of Collembola. To increase the catch, traps were set for another four 6-h periods on 2–3 June and catches from the same 6-h period on each day were pooled (Table 1). This trapping procedure was repeated on a further six sampling occasions from June to August, with the catch from each 6-h period being the aggregate from two days' trapping (Table 1) and hence representing a total of 12 trap-hours.

2.2.3. Sweep net samples

A sweep net with sampling area 0.071 m^2 was used to collect Collembola from the top of the crop canopy on four occasions during the summer (Table 1). On each occasion, 50 randomly-located sweeps were taken such that the top of the net was level with the top of the wheat foliage, avoiding the location of each pitfall trap by at least 1 m. Catches from five sweeps were pooled to give 10 sweep samples at each of four times in a diel period (00.00, 06.00, 12.00 and 18.00 h). Each sample represented ca. 0.05 m^3 of the upper crop foliage. Sweep samples were taken on only four occasions because of the risk of depleting crop-inhabiting Collembola (see Section 4.1). For each sampling method, the start times were varied between the dates (Table 1) to reduce any impact of sampling sequence on catches.

2.2.4. Estimation of activity

It is difficult meaningfully to compare pitfall and suction catches because the area sampled by pitfall traps is not known, and would differ among species depending upon their rates of movement. Another unknown is their efficiency for capturing Collembola, which could vary among species (cf. Halsall and Wratten, 1988). By using the same number of samples in all comparisons, however, diel changes in the relative catch size of the two methods should provide information on relative changes in collembolan activity. For this purpose, abundance estimates for each 6-h pitfall trapping period were obtained by averaging the suction counts obtained at the start and end of the 6-h period. Suction and pitfall catches were not always taken on the same days within each sampling occasion (Table 1), but nevertheless a consistent pattern of diel changes in the relative catch size of suction and pitfall samples occurred (see Section 3.2).

2.2.5. Microclimate measurements

A data logger with humidity and temperature probes was used to record continuously air temperature and humidity within 0.5 cm of the soil surface in the centre of the study area. Problems with data download from the logger restricted temperature measurements to the first four sampling occasions indicated in Table 1, while humidity data were available only for the first occasion (1–3 June). Screen temperature maxima and minima obtained from a site ca. 6 km from the study field were used to supplement the local microclimatic measurements and indicated that, during the period of the study, maxima were consistently recorded in the afternoon and minima at night (G.K. Frampton, unpublished data).

2.3. Data analysis

Two statistical approaches were used to analyse the Collembola counts obtained by suction and pitfall sampling. Univariate analysis of variance for each species and sampling date tested the null hypothesis that Collembola counts did not differ between sampling times within a diel period. For analysis at the community level, PRC analysis was used to display graphically temporal changes in species composition. PRC analysis is a multivariate technique which has advantages over traditional ordination techniques (Section 2.3.2). Sweep catches of Collembola were analysed only with the univariate approach because few species were captured using this method.

2.3.1. Univariate analysis

For each species, one-way analysis of variance with four levels of the fixed factor 'diel sampling time' was performed on collembolan counts at each sampling occasion. The data counts x were normalised before analysis, using $\ln(x + 1)$. For each level, there were five replicates for suction samples and 10 for pitfall and sweep samples. In cases where the null hypothesis was rejected, Fisher's multiple comparisons test (Fisher, 1925) was used to identify sampling times whose catches differed significantly when the experiment-wise error rate per sampling date was set to $\alpha = 0.05$ ($P < 0.008$ for individual contrasts) (Dunn-Šidák method; Sokal and Rohlf, 1995).

2.3.2. Principal response curves analysis

PRC analysis is a recently-developed derivative of the multivariate ordination technique redundancy analysis (RDA) that can provide a clear graphical display of temporal changes in community structure (Van den Brink and Ter Braak, 1997, 1998, 1999; Frampton et al., 2000a,b). In PRC analysis, the statistical model for the species abundance data is

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

where $Y_{d(j)tk}$ is the abundance of species k in replicate j of diel sampling time d at sampling date t, $Y_{\underline{0}tk}$ is the mean abundance of species k on date t at a chosen reference diel sampling time d_0, c_{dt} is a basic response pattern for every diel sampling time 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. 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 how closely the response of each individual taxon matches the overall community response as displayed in the PRC diagram.

In all previous studies that have used PRC analysis, an experimental 'control' treatment level was used as the reference treatment level $d = 0$ (Van den Brink and Ter Braak, 1997, 1998, 1999; Frampton et al., 2000a,b). Here, however, an obvious 'control' treatment does not exist among the diel sampling times. Although a reference level must be specified in PRC analysis (Ter Braak and Šmilauer, 1998), the choice of reference does not limit the visual and quantitative treatment contrasts that can be made using a PRC diagram. Accordingly, the 18.00 h sampling time (suction samples) or 18.00–00.00 h sampling period (pitfall catches) were nominated as arbitrary reference levels in the PRC analyses; these are the times at which largest collembolan catches most often occurred (see Section 3).

Quantitative interpretation of the relative abundance of a species at different diel sampling times compared with the reference time can be obtained from the values of b_k and c_{dt} in a PRC diagram. The expression

$$\exp(b_k c_{dt}) \tag{2}$$

gives the fitted difference in abundance of species k under treatment d at time t relative to the reference time, and can also be used to interpret differences in abundance among diel sampling times other than the reference time (examples are given in Section 3.4).

In addition to providing a concise graphical summary of changes in community structure, PRC analysis indicates the part of the total variance in the data set that is explained by treatment effects (here, the effects of diel sampling times). A PRC diagram aims to maximise the amount of variance due to treatments that is displayed; the larger the displayed proportion of the variance, the more closely will the fitted relative abundance of individual taxa inferred from the diagram match the observed relative abundance (Ter Braak and Šmilauer, 1998). Estimates of c_{dt} and b_k were obtained for $\ln(x + 1)$-transformed Collembola counts x, using the software program CANOCO 4 (Ter Braak and Šmilauer, 1998), with five replicates of each suction sampling time and 10 replicates of each pitfall trapping period (Section 2.2). The values of c_{dt} were used to plot PRC diagrams to show the overall temporal collembolan community changes. The significance of each PRC diagram was tested using Monte Carlo permutation tests (9999 permutations), 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. $c_{dt} \times b_k = 0$ for all t, d and k). A second series of permutation tests was performed for each sampling date to test the null hypothesis that differences indicated by the PRC diagram between diel sampling times are not statistically significant. In these tests, the number of permutations used was 9999 for pitfall samples and 252 for suction samples (in the latter case limited by the number of replicates). As in the univariate analyses (Section 2.3.1), the experiment-wise error rate per sampling date was maintained at $\alpha = 0.05$.

3. Results

3.1. Univariate analysis

Thirteen collembolan taxa were recorded during the study (Table 2). The species composition is typical of European arable land, in which *L. cyaneus* is often the dominant species (e.g. Kovác, 1994; Alvarez et al., 2001). Counts obtained by suction sampling (Fig. 1), pitfall trapping (Fig. 2) and sweep sampling (Fig. 3) varied both within diel periods and between sampling dates. Differences in counts between diel sampling times were statistically significant on several sampling dates for suction and pitfall catches of individual species, and also for counts pooled as Arthropleona, Symphypleona and total Collembola. The largest variation in captures within a diel period was for *L. cyaneus*, the most abundant collembolan taxon in suction and pitfall samples and which dominated the Arthropleona catch (Figs. 1 and 2). Assuming that the majority of these Collembola captured by suction sampling originated from the surface of soil or low-growing weeds (Table 2), an estimate of collembolan density is the total abundance in suction catches expressed per square metre of the ground sampled. On the third sampling occasion (29–30 June; Table 1), the estimate of density for *L. cyaneus* was higher at 18.00 h on 29 June than at 00.00 h on 30 June by ca. 250 per 0.46 m^2 (Fig. 1a), while for the total Arthropleona, the difference between these times was ca. 400 per 0.46 m^2 (Fig. 1g), equivalent to changes within 24 h of ca. 540 and 870 m^{-2}, respectively. Sweep catches also varied within a diel period, but only on one sampling occasion, after which Collembola counts were negligible. For most Collembola, catches in suction samples at the end of June (sampling occasion 3) were markedly higher at 18.00 h than at the other sampling times, but the pattern of catches was more variable in pitfall traps (Fig. 2). Peak pitfall catches during this sampling occasion were in the morning for *S. aureus* (Fig. 2f), in the afternoon for *L. cyaneus* (Fig. 2a), and in the evening for *S. elegans* (Fig. 2e). Overall, pitfall catches throughout the summer were highest in the afternoon and evening (12.00–00.00 h) (Fig. 2g–i). In contrast to suction and pitfall samples, sweep catches were dominated by Symphypleona, principally *Deuterosminthurus* spp. (Fig. 3).

Table 2
Overall captures of Collembola during the study in pitfall traps, suction and sweep samples[a]

Taxon	Suction		Pitfalls		Sweeping	
	Total	%	Total	%	Total	%
Sminthurus viridis (L.)	25	0.2	8	0.1	47	8.2
Sminthurinus elegans (Fitch)	883	5.8	630	6.5	0	0
Sminthurinus aureus (Lubbock)	99	0.7	117	1.2	0	0
Deuterosminthurus spp.	816	5.4	46	0.5	504	88.1
Bourletiella hortensis (Fitch)	3	<0.1	106	1.1	0	0
Sminthuridinae	20	0.1	620	6.4	0	0
Isotoma viridis Bourlet	2330	15.4	2095	21.7	1	0.2
Isotomurus spp.	4	<0.1	3	<0.1	0	0
Ceratophysella denticulata (Bagnall)	20	0.1	117	1.2	0	0
Lepidocyrtus cyaneus Tullberg	8962	59.4	5608	58.2	20	3.5
Pseudosinella alba (Packard)	1913	12.7	289	3.0	0	0
Pseudosinella decipiens Denis	22	0.1	0	0	0	0
Orchesella villosa (Geoffroy)	0	0	2	<0.1	0	0
Total						
Order Symphypleona	1846	12.2	1527	16	551	96.3
Order Arthropleona	13251	87.8	8114	84	21	3.7
All Collembola	15097		9641		572	

[a] Catches (with all replicate counts added together) are from a total of 3360 pitfall-trap-hours, 100 suction samples (nozzle area 0.46 m^2) and 160 sweep samples (each ca. 0.05 m^3).

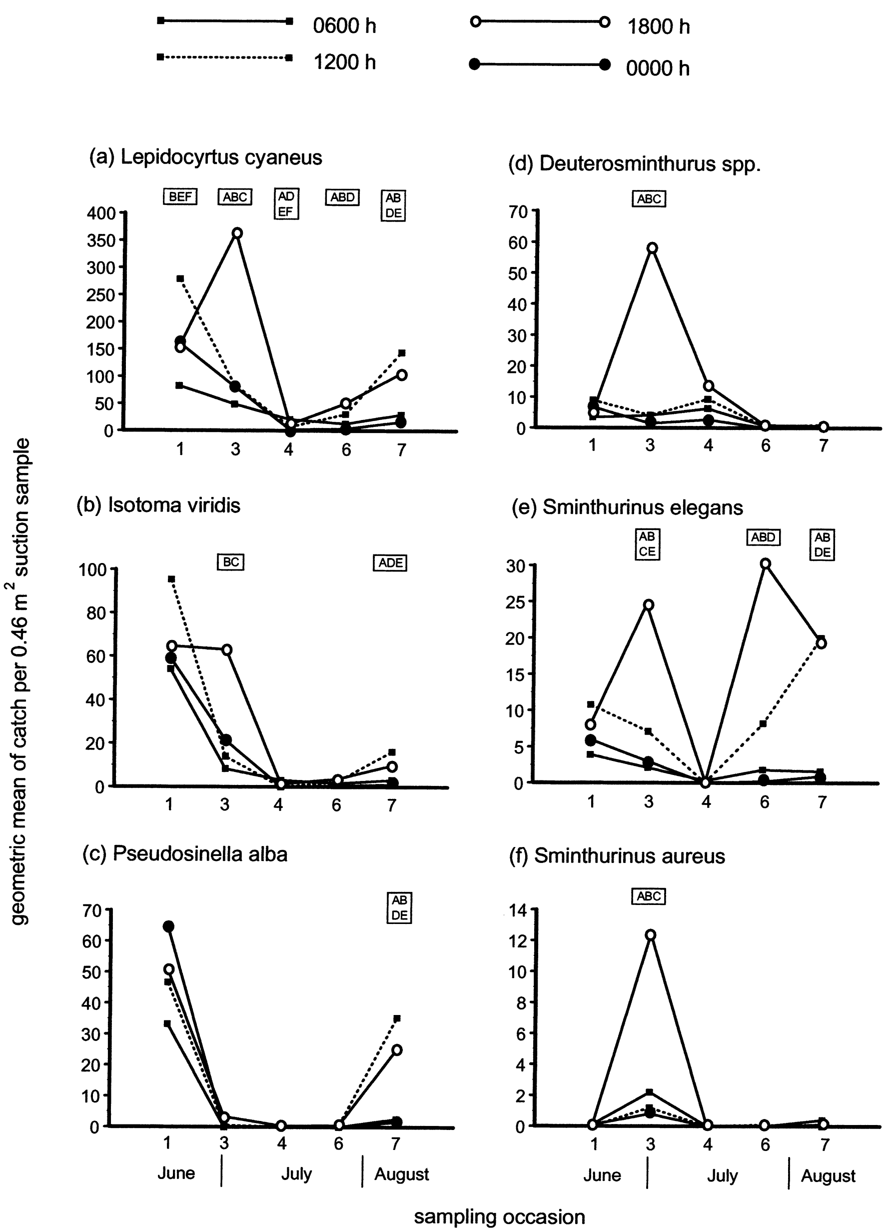

Fig. 1. Suction catches of Collembola at four sampling times on each of five sampling occasions in summer. Letter codes (A–E) indicate pairs of diel sampling times that differ significantly in their geometric mean Collembola counts ($P < 0.008$ for individual contrasts): A: 18.00 and 00.00 h; B: 18.00 and 06.00 h; C: 18.00 and 12.00 h; D: 12.00 and 00.00 h; E: 12.00 and 06.00 h; F: 06.00 and 00.00 h. Note differing axis scales.

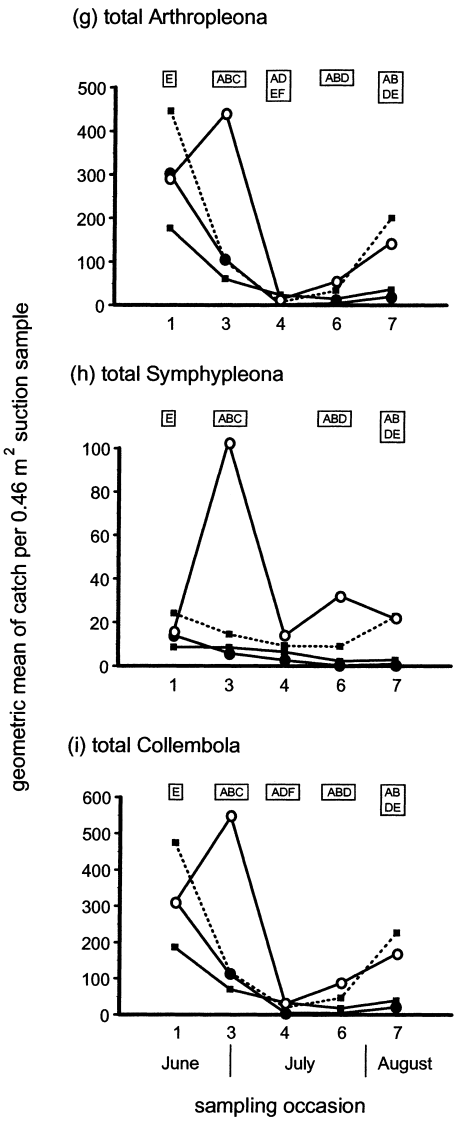

Fig. 1. (*Continued*).

3.2. Comparison of suction and pitfall sampling methods

Species composition of pitfall and suction catches was broadly similar (Table 2). One species (*P. decipiens*) was captured only in suction samples and another (*B. hortensis*) almost exclusively in pitfall traps, although catches of these species per sample were low (Table 2). Patterns of diel variation in the relative catch size of pitfall and suction samples are evident, particularly among Symphypleona (Fig. 4). The proportion of the Symphypleona catch that was obtained from pitfall traps was very low on two sampling occasions (1 and 4) at the start of June and in mid-July, when collembolan activity appears to have been low at all sampling times (Fig. 4a). Within the remaining three sampling occasions, the relative catches of suction and pitfall samples exhibited a consistent pattern of change during the diel period. The contribution made by pitfall traps to the overall Symphypleona catch was highest in the period after midnight (00.00–06.00 h) and then declined to a minimum in the afternoon (12.00–18.00 h) (Fig. 4a). Such diel changes in the relative contribution of pitfall and suction samples to the total catch were not evident for Arthropleona (Fig. 4b).

3.3. Effects of microclimate

Limited availability of temperature and humidity data (Section 2.2.5) precluded a detailed analysis of the effects of diel variation in crop microclimate on Collembola catches. However, a significant positive linear regression of pitfall catches of *L. cyaneus* on mean soil surface temperatures for each pitfall trapping period was evident when counts from the first four sampling occasions (June to mid-July) were analysed (Fig. 5). No regressions of Collembola catches on temperature were significant for any other species or sampling method. The limited microclimate data which were available for 1–3 June (Frampton, 1989) indicated an inverse relationship between relative humidity and soil surface temperature. Rainfall did not occur during, or within 12 h of any of the sampling periods.

3.4. Principal response curves

PRC diagrams for suction samples (Fig. 6) and pitfall captures (Fig. 7) concisely show changes through the summer in the diel variability of collembolan community composition. Of the total variance in the suction sample catches, 61% is explained by sampling date and 24% by diel sampling time. A significant proportion of this variance (76%; $F = 67.6$; $P \leq 0.0001$) is displayed in the first PRC diagram (Fig. 6). For pitfall catches, 47% of the total variance is explained by sampling date and 16% by diel sampling

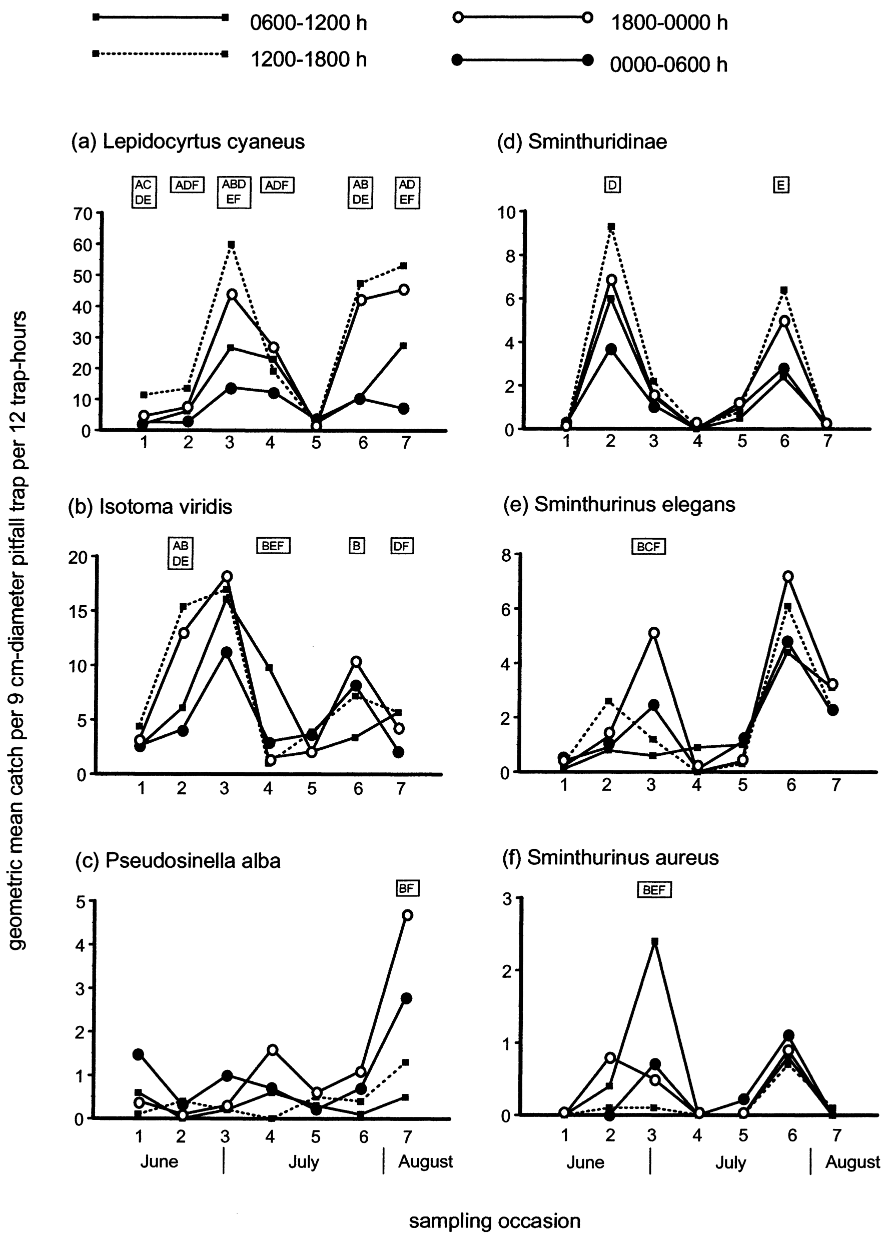

Fig. 2. Pitfall trap catches of Collembola in four diel sampling periods on each of seven sampling occasions in summer. Letter codes (A–E) indicate the start times for pairs of 6 h sampling periods that differ significantly in their geometric mean Collembola counts ($P < 0.008$ for individual contrasts): A: 18.00 and 00.00 h; B: 18.00 and 06.00 h; C: 18.00 and 12.00 h; D: 12.00 and 00.00 h; E: 12.00 and 06.00 h; F: 06.00 and 00.00 h. Note differing axis scales.

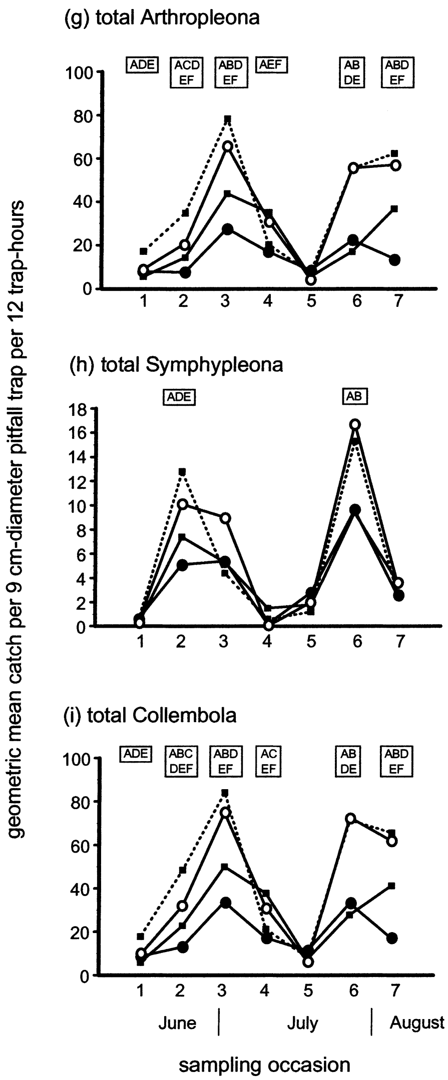

Fig. 2. (*Continued*).

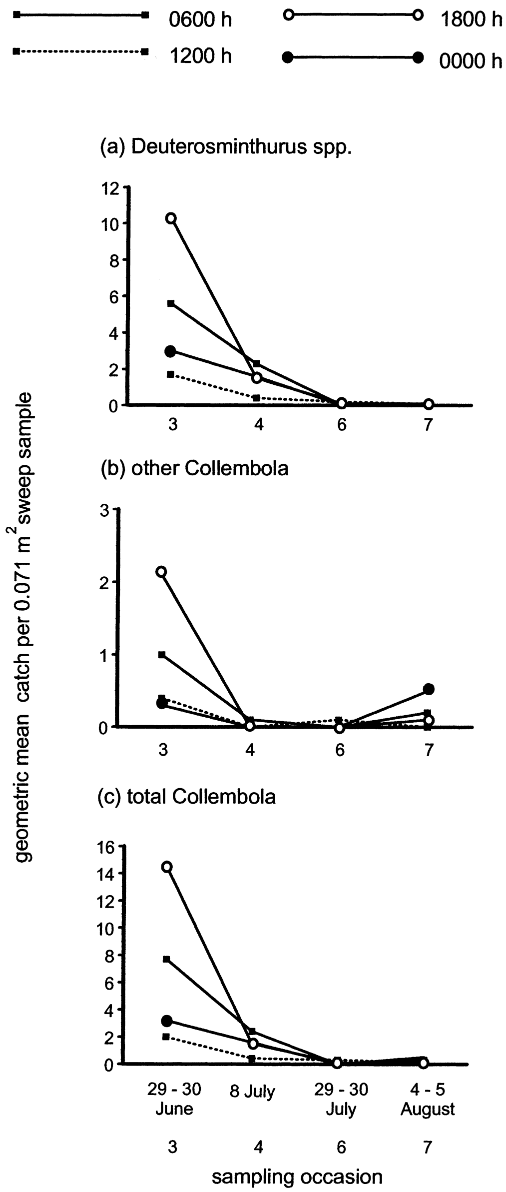

Fig. 3. Sweep samples of Collembola at four sampling times on each of four sampling occasions in summer. Geometric mean catches that differed significantly ($P < 0.008$ for individual contrasts) were 12.00 and 18.00 h for *Deuterosminthurus* spp. and 18.00 and 00.00 h for the total Collembola. Note differing axis scales.

time, with a significant proportion of this variance (51%; $F = 46.8$; $P \leq 0.0001$) displayed in the second PRC diagram (Fig. 7). Values of c_{dt} indicate the deviation of species composition from the reference (the 18.00 h catch for suction samples or the 18.00–00.00 h pitfall catch). For suction samples, most values of c_{dt} are negative, indicating that catches at 00.00, 06.00 and 12.00 h were mostly lower than at 18.00 h (Fig. 6); the pattern for pitfall captures is less consistent (Fig. 7). The large difference in the suction catch between the reference and other diel times is clearly evident on 29–30 June (sampling occasion 3) (Fig. 6). Within-date permutation tests show that on most sampling dates, differences in collembolan

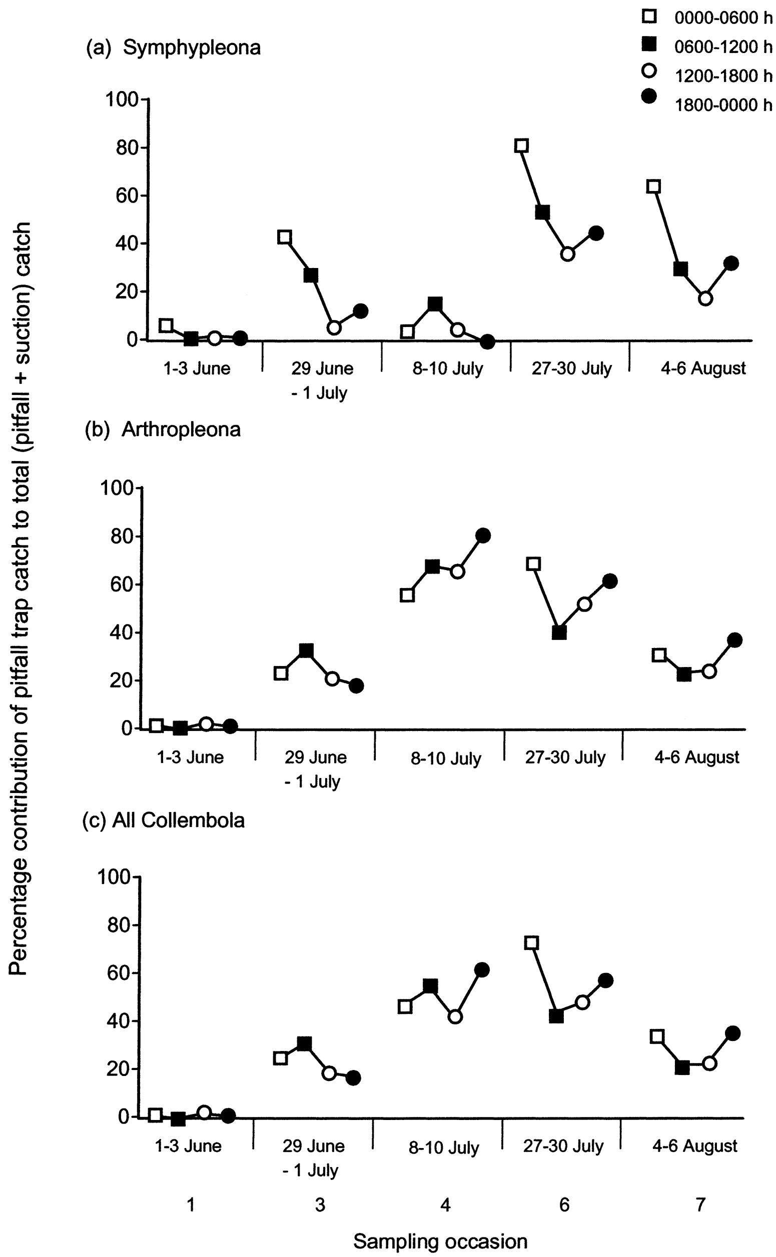

Fig. 4. Proportional contribution of pitfall catches (estimates of combined abundance and activity) and suction samples (estimates of abundance) to the total (suction + pitfall) Collembola catch at four diel sampling times on each of five sampling dates in summer.

community composition among diel sampling times are statistically significant (Figs. 6 and 7).

The relationship of individual species with the pattern of changes in community composition displayed in the PRC diagrams is given by the species weights b_k. All weights are positive, hence all species are positively associated with the pattern of changes in relative abundance displayed in the PRC diagrams; a negative weight would indicate a species' response to be the opposite to that shown. Species with the highest weights are most likely to follow the pattern of changes in relative abundance in the PRC diagram; those with low weights (<0.5) do not contribute strongly to the overall community response which is displayed, either because they are rare in samples or exhibit a response pattern different to that displayed in the diagram. For this reason, species with low weights are not shown in the PRC diagrams; all excluded species had low counts. Changes in the abundance of individual species can be interpreted quantitatively using the values of c_{dt} and b_k given in the PRC diagrams (Eq. (2); Section 2.3.2).

Thus, for suction catches of *L. cyaneus* on 4–5 August (sampling occasion 7), the PRC diagram (Fig. 6) predicts that the catch at 06.00 h would be $\exp(1.76 \times -0.86) = 0.22$ times the catch at the reference time (18.00 h). This agrees well with the actual

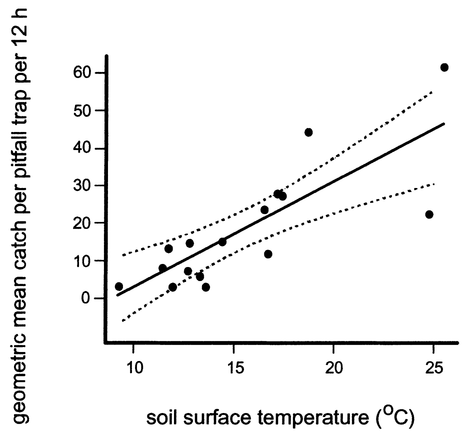

Fig. 5. Relationship (with 95% confidence bonds) between soil surface temperature and pitfall catches of *L. cyaneus* on four sampling occasions in summer. The regression of *L. cyaneus* catch (y) upon temperature (x) is significant ($y = -25+2.8x$; $R^2 = 60.6$; $F = 21.5$; $P < 0.001$).

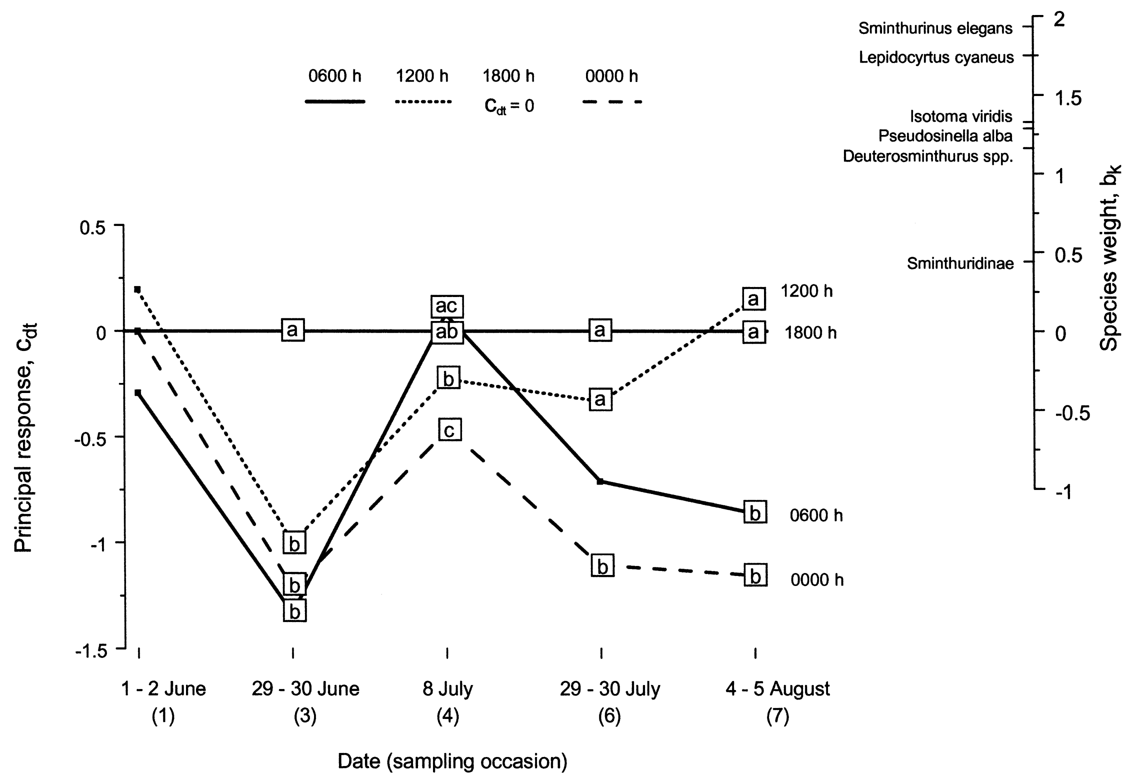

Fig. 6. PRC diagram and species weights b_k for suction-sampled Collembola, showing diel variation in species composition on five sampling occasions in summer. At each date, values of c_{dt} differ significantly between sampling times that do not share the same letter code (a-c) ($P < 0.008$ for individual contrasts); shared or omitted letter codes denote contrasts that do not differ significantly. For interpretation of b_k and c_{dt}, see text (Section 2.3.2).

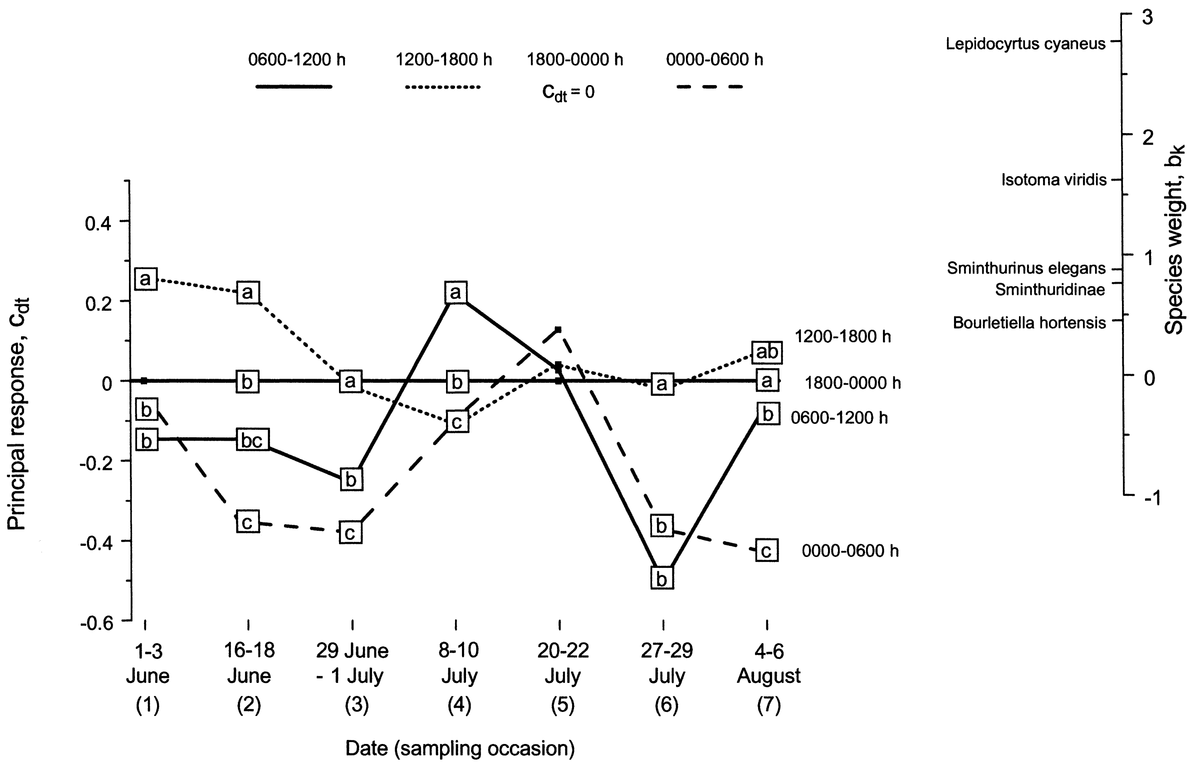

Fig. 7. PRC diagram and species weights b_k for pitfall-sampled Collembola, showing diel variation in species composition on seven sampling occasions in summer. At each date, values of c_{dt} differ significantly between 6 h sampling periods that do not share the same letter code (a-c) ($P < 0.008$ for individual contrasts); shared or omitted letter codes denote contrasts that do not differ significantly. For interpretation of b_k and c_{dt}, see text (Section 2.3.2).

data (Fig. 2a), in which the geometric mean counts on the 4–5 August were 30 and 106, respectively, for the 06.00 and 18.00 h catches (relative abundance, 0.28). Similarly, the PRC diagram predicts that the 12.00 h suction catch of *L. cyaneus* on 4–5 August would be $\exp(1.76 \times 0.15) = 1.30$ times that at 18.00 h, which is in close agreement with the observed relative abundance of 1.36 (geometric mean counts were 144 and 106, respectively; Fig. 2a). The calculation of fitted relative abundance between two diel sampling times other than the reference time (here 18.00 h) is also straightforward. In the above example for suction catches of *L. cyaneus* on 4–5 August, the abundance at 06.00 h relative to 12.00 h is given by $\exp(b_k(c_{dt1} - c_{dt2}))$, i.e. $\exp(1.76 \times (-0.86–0.15)) = 0.17$. It may alternatively be obtained from the ratio of the fitted abundances at 06.00 and 12.00 h relative to the reference, i.e. $0.22/1.30 = 0.17$. Again, in this example, the fitted relative abundance is close to the observed relative abundance of 0.21 (geometric mean counts for 06.00 and 12.00 h were 30 and 144, respectively; Fig. 2a).

4. Discussion

A number of workers have investigated diel patterns of collembolan activity, but the findings presented here are the first detailed study of diel changes in community composition in a cereal crop. Before attempting to interpret these findings, some potential limitations of the experimental design and sampling methods should be considered.

4.1. Study design and limitations

A problem with estimating collembolan abundance or activity at fine temporal scales is that short sampling periods may yield low catches. To overcome this, samples can be pooled for similar sampling times on different dates, as has been done with time-sorting pitfall traps (e.g. Desender et al., 1984). Alternatively, large numbers of replicate traps can be used at each sampling time, but with the risk of depleting the fauna unless traps are widely spaced (e.g. Digweed et al., 1995). However, sampling a larger area could increase spatial heterogeneity in the data set, as some collembolan species have restricted spatial distributions within arable fields (Frampton, 2000) and diel activity patterns can vary with habitat type (Brand, 1979). The fact that all sampling was conducted within a 15 m × 15 m area of the wheat field could have implications for interpretation of the results if sampling led to depletion of arthropods, or if sampling with one method influenced catches obtained with another. It is probable that just the act of walking in the field would have been sufficient to have affected pitfall catches of Collembola (Joosse and Kapteijn, 1968), but this should not have induced temporal bias as care was taken to ensure that any physical disturbance to the crop and ground was similar at all sampling times. Although depletion of Collembola by sampling could possibly account for the observed decrease during July and August in suction catches (Fig. 1) and sweep catches (Fig. 3), this is improbable for four reasons: (1) at each sampling time only 1% of the available ground area was suction sampled and ca. 0.3% of the volume of upper crop foliage swept with a net; (2) the study area was open to recolonisation by immigration from the surrounding field; (3) pitfall catches of some Collembola were as high in August as they had been during June and (4) examination of some ad hoc suction and sweep samples taken in other parts of the field suggested low suction and sweep catches in August were not specific to the study area. The possibility that *Deuterosminthurus* spp. knocked off crop plants by sweep sampling would have affected pitfall catches is not borne out by the relatively low counts of this genus which were caught in pitfall traps. It is possible that the temporal resolution of sampling would have been too coarse to detect some diel changes in activity or abundance (e.g. Bowden et al. (1976) observed that most climbing activity by Collembola was completed within 5 h), but the catches nevertheless reveal consistent patterns, with implications for sampling strategy (Section 5).

The order of pitfall sampling employed during 16–18 June (Table 1) raises the possibility that if the fungicides applied on 16 June (Section 2.1) affected Collembola, an increase or decrease in catches in the period immediately after application could be manifest as diel variation in catches during 16–18 June (sampling occasion 2). Effects of the fungicides on the diel pattern of catches can be ruled out, however, because the same pattern of diel variation as occurred following fungicide application was more strongly evident at the end of June when no chemicals were used. A final point concerning the restrictions of the experimental design is that sampling was necessarily confined to dry weather (rain fell during the summer, but not within 12 h of the sampling occasions). These findings thus may not be representative of wetter weather conditions, but nevertheless represent conditions typical of the majority of summer days in southern England.

4.2. Collembolan activity patterns

The positive correlation between temperature and the pitfall catch of *L. cyaneus* is direct evidence for the importance of temperature as an abiotic factor, but was not detected for other species. Joosse (1965) found no clear relation between temperature and pitfall catches of *L. cyaneus* in woodland, whereas other species exhibited either positive or negative correlations. The findings presented here also differ from hers in that *L. cyaneus* in woodland was more active at night, but in the wheat crop both its above-ground abundance and activity were consistently highest during the day. Nocturnal activity is generally more frequent among forest than field-inhabiting macroarthropods (Williams, 1960; Luff, 1978), but too few data are available to be sure whether this is also a general pattern in Collembola. In the wheat crop, collembolan activity was predominantly diurnal (apart from activity of *P. alba* and *S. aureus* being highest between 18.00 and 06.00 h on a minority of sampling occasions). Although nocturnal activity of Collembola has been reported in other work, e.g. in cereals (G.P. Vickerman, unpublished data), woodland (Joosse, 1965) and an urban habitat (Moon and Gough, 1972), the only detailed information available on collembolan diel activity patterns in open fields, which was based on data pooled over sampling dates, suggests that the majority of epigeic species are active diurnally, or throughout both day and night (Desender et al., 1984).

The suction catches of Collembola obtained in this work indicate abundance on the soil surface and vegetation, but provide no information on below-ground densities. Given that short time intervals elapsed between sampling times, consistent diel changes in above-ground abundance cannot be explained by cycles of recruitment or mortality. Instead, horizontal or vertical movement probably occurred between exposed soil, or vegetation, and refuges where the insects would have been inaccessible to sampling. Several of the species captured (*S. aureus*, *I. viridis*, *C. denticulata* and *L. cyaneus*) have been found at depths exceeding 8 cm in undisturbed grassland soils (Dhillon and Gibson, 1962; Curry, 1971), and it has been suggested that vertical penetration of Collembola in cultivated soils is likely to be at least as deep as in undisturbed soils (Filser and Fromm, 1995). Some of the captured species have also been observed on wheat plants and crop weeds (e.g. Curry, 1976; Frampton, 1999). Collembola may exhibit climbing behaviour in response to favourable conditions of humidity (Bauer, 1979), ascending plants early in the morning or at night when temperatures are relatively low (e.g. Davies, 1925), or in response to rainfall (Bowden et al., 1976). Although the data do not identify the ecological mechanism, a low ratio of activity to above-ground abundance of Symphypleona in the late afternoon would be consistent with aggregation of individuals in favourable microhabitats (e.g. upon vegetation) in response to unfavourably high temperatures and low humidity at the soil surface (Joosse and Groen, 1970; Joosse, 1971). Conversely, the higher ratio of activity to above-ground abundance after midnight could reflect dispersal from aggregation sites as soil surface ambient temperature and humidity conditions became more favourable (e.g. Desender et al., 1984). An important point here is that the catches of Symphypleona obtained by pitfall sampling gave no reliable indication of short-term changes in above-ground abundance. The large diel variation in suction catches was unexpected, particularly as peak catches were in the late afternoon when maximum soil-surface and air temperatures were recorded (G.K. Frampton, unpublished data). Vertical migration in soil is usually downwards when temperature and humidity become unfavourable at the surface (McBrayer et al., 1977; Whitford et al., 1981; MacKay et al., 1987; Hopkin, 1997), so a smaller suction sample catch would have been expected. A possible explanation for the larger afternoon catches could be that Collembola aggregated in areas of high relative humidity, e.g. upon vegetation where they would have been readily captured by suction sampling. However, to confirm such behaviour would require a better understanding of how vegetation (weeds or crop plants) affects the efficiency of Collembola suction sampling. If the position on vegetation of foliage-dwelling species such as *Deuterosminthurus* spp. affects their capture efficiency, relatively small-scale redistribution on plants (e.g. between abaxial and axadial leaf surfaces, stems and inflorescences) might explain the large diel variation in local abundance indicated by suction catches.

Assuming that the Collembola captured in suction samples would otherwise have been available to predators, e.g. on soil or leaf surfaces, the diel variation in the above-ground abundance of Arthropleona by up to 870 m^{-2} within 12 h suggests that availability of Collembola to predators could change considerably within a diel period. The overall tendency for collembolan abundance to be higher during the day than at night might have an impact on biocontrol of aphids because availability of Collembola has been implicated in reduced aphid consumption by polyphagous predators (e.g. Chiverton and Sotherton, 1991), which in cereals consume aphids mainly at night (Vickerman and Sunderland, 1975). Given the importance of Collembola in food webs, and the potentially complex diel changes in predator–Collembola interactions that can occur (Ernsting et al., 1977), it is clear that a better understanding of the short-term temporal dynamics of collembolan predation is needed.

4.3. Principal response curves

This study has illustrated how PRC analysis can be applied to an experimental design in which pair-wise comparisons among all treatment levels are of interest. Visual and quantitative interpretation of changes in community composition from the PRC diagrams is straightforward, and not dependent upon the treatment level chosen as the reference level (Section 3.4). Because relatively few species were captured, individual species' data is presented along with the community-level analysis to illustrate the quantitative interpretation of the PRC diagrams. However, the PRC diagrams alone could have been used to infer patterns of variation in relative abundance of the individual species. PRC diagrams are particularly appropriate for displaying changes in communities that contain a large number of species where it would not be feasible to separately display the individual species' responses (e.g. Van den Brink and Ter Braak, 1999). The species weights displayed with a PRC diagram show whether individual species exhibit the same response as the overall community, or an opposite response, and hence can provide an insight into ecological interactions. In the current study, the lack of negative values of the species weights indicates that no consistent nocturnal activity was detected among any of the Collembola taxa captured in suction samples.

5. Conclusions

For most of the epigeic species captured, suction or sweep samples collected in the late afternoon (18.00 h) generally gave maximum collembolan catches. However, PRC analysis shows that species composition of pitfall catches was more variable, both within and between sampling dates. Although pitfall traps are undoubtedly useful for detecting general patterns of collembolan activity, the catch is not a reliable indicator of abundance over short trapping periods. Care is advised for the interpretation of short-term pitfall trap catches because the effects of temperature on the catch evidently vary between species and with habitat type. The possible effects of diel variation in the abundance of Collembola on their exposure to agrochemicals and their predation by macroarthropods are poorly understood and warrant more detailed investigation. Interpretation of the ecology of farmland Collembola is currently also limited by a lack of information on how vegetation structure affects sampling efficiency in arable fields.

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