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Epigeal Collembola in arable fields: their ecology in relation to the effects of pesticides

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ABSTRACT

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Epigeal Collembola in arable fields: their ecology in relation to the effects of pesticides

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The ecology of arable springtails (Collembola) was investigated in relation to pesticide exposure and recovery. *Lepidocyrtus* spp., *Isotomurus* spp., *Bourletiella hortensis*, *Isotoma viridis*, and *I. notabilis* overwintered as surface-active adults within fields where they could potentially be exposed to pesticide deposition at a time when little or no crop cover was present. *Sminthurus viridis* and *Sminthurinus elegans* overwintered as eggs in the field soil, where exposure to sprayed winter pesticide applications would be expected to be lower than for surface-active species. The eggs of *S. viridis, S. elegans* and *B. hortensis* from field soils were resistant to periods of drought, although resistance varied among species. This study provided the first evidence for drought tolerance in eggs of *S. viridis, S. elegans* and *B. hortensis* in northern European arable habitats; viable eggs survived a four-month period of simulated drought in the laboratory. Drought resistance of some species is likely to alter the community composition in fields and hence affect the availability of vulnerable species for monitoring pesticide non-target effects.

S. elegans, S. viridis and *I. viridis* dispersed into arable fields from an adjacent hedgerow, providing the first evidence that hedgerows may be important sources for collembolan recolonisation of arable fields. *B. hortensis, Isotomurus* spp. and *Lepidocyrtus* spp. were found to recover from population sources within the field itself. Certain species including *B. hortensis, Isotomurus* spp. and *E. multifasciata* were consistently found in the vicinity of hedgerows and may be unlikely to be true arable field species, and hence of limited use in studies monitoring pesticide effects.

Collembolan abundance and community composition were compared in fields managed under organic, conventional and integrated regimes to assess the effects of farming systems. Differences in community composition were identified among regimes, although no individual species or species assemblage was indicative of any of the farming management systems. Abundance of individual species varied among fields and regions, suggesting that the scale at which comparisons are made may affect the likelihood of detecting pesticide effects. The results of this study are discussed with respect to the use of Collembola for ecological monitoring of non-target pesticide effects.

CONTENTS

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1. General introduction: a review of the ecology of Collembola in European agroecosystems.

1.1 Introduction

Long-term studies have highlighted the vulnerability of Collembola to some pesticides (e.g. Boxworth - Frampton *et al.* 1992, SCARAB - Frampton 1999, FAM - Filser *et al.* 1995) and suggested that they could be more suitable for detecting non-target pesticide effects than currently used ecological monitors. This vulnerability, together with the eurytopic nature of different species (e.g. Christiansen & Bellinger 1995), makes Collembola a potentially suitable group for monitoring non-target pesticide effects. However, relatively little is known about collembolan ecology in arable farmland; such information would enable us to assess their potential as indicator species. The vulnerability of a species is a function of its intrinsic sensitivity to the chemical, its degree of exposure to that pesticide (Brown 1986, 1988), and its ability to recover after an application (van Straalen 1994). In this thesis I investigated aspects of collembolan ecology which determine exposure and recovery, and hence vulnerability to pesticides.

The focus of the first chapter is to consider aspects of collembolan biology and ecology in arable fields likely to determine vulnerability to pesticide applications, and summarise current information on the sensitivity of different species to individual pesticides. The content of successive chapters is briefly outlined in section 1.8.

1.2 A brief background to Collembola

Collembola (Hexapoda) are small members of the soil fauna, with the largest measuring a maximum of 10 mm in length. Most species possess a characteristic furcula

(springing organ) and collophore (breathing tube). They differ from insects in having a maximum of six abdominal segments at all developmental stages, entognathous mouthparts, and a variable number of ocelli rather than compound eyes (Richards & Davies 1977, Eisenbeis & Wichards 1987, Gullan & Cranston 1994). The current states of taxonomy, biology and ecology for Collembola are beyond the scope of this chapter. An extensive recent review can be found in Hopkin (1997a). Other useful summaries of collembolan taxonomy, ecology and biology are available in Christiansen (1964), Cassagnau (1990a, 1990b) and Rusek (1995).

Collembola are widespread and numerous in agroecosystems (e.g. up to 10000 m^{-2}, Kovac & Miklisova 1997), with a wide diversity (e.g. up to 108 species were identified from all the sampling sites in a study of arable fields by Kovac & Miklisova 1997). Epigeal species (surface and plant-dwelling) such as *Orchesella cincta* (Linnaeus) are found on soil surfaces and leaf litter; hemiedaphic species are found in shallow soil layers and on the soil surface (e.g. *Hypogastrura* spp.); and euedaphic species such as the Onychiuridae are found in deep soil (see Hopkin 1997a for a general review of collembolan biology). The spatial distribution of Collembola is determined by many factors mediating the results of interspecific competition (Vegter 1983, Hägvar 1990). These factors include soil water content and availability (Verhoef 1981, Verhoef & van Selm 1983), soil pH (Hägvar & Abrahamsen 1980, Kopeszki & Jandle 1994, van Straalen & Verhoef 1997), the extent of vegetation cover, soil depth and type, and local variations in temperature and food availability (Pozo 1986). Collembola usually form aggregations (e.g. Usher 1969, Joosse 1970, 1971) and a number of possible explanations have been suggested (e.g. favourable local conditions for breeding, or a lack of dispersal ability by individuals; the latter hypothesis was supported by an investigation carried out by Vegter *et al.* 1988a, 1988b on Entomobryidae in woodland). The spatial

distribution of Collembola should be considered when planning sampling schedules to monitor pesticide effects (see Frampton 1994).

1.3 The role of Collembola in agroecosystems

There is contradictory evidence for the importance of Collembola in arable ecosystems. In this section the role of Collembola as detritivores, biocontrol agents, agricultural pests and prey species for beneficial arthropods will be discussed.

1.3.1 Collembola as detritivores

The majority of Collembola feed on fungal hyphae and detritus (see Hopkin 1997a and references therein). In arable fields some studies have suggested that they are not of great importance in decomposition, soil formation or in nutrient dynamics, as they only constitute two to ten percent of the animal biomass (Petersen & Luxton 1982, Petersen 1994, Martikainen *et al.* 1998). However, other studies have suggested that they contribute significantly to humification and decomposition (Hendrix *et al.* 1986, van Amelsvoort *et al.* 1988) and nutrient dynamics (Mebes & Filser 1998). As detritivores, mycophages and bacteriophages it is likely that Collembola play an important part in the breakdown of large particles of organic matter (Seastedt 1984), thereby improving the porosity of soils and hence its drainage. Reducing particle size increases the surface area available to bacteria and microorganisms, and as such indirectly aids the process of decomposition. Collembolan selective grazing of fungi could also have long-term consequences upon litter decomposition

(Jones *et al.* 1998). Hägvar (1998) recently reviewed the importance of collembolan species diversity in a soil ecosystem context. Since there is conflicting evidence on the mechanisms of action and the degree of importance of the collembolan fauna at different soil depths, this area merits further investigation.

1.3.2 Collembola as beneficial species

The Collembola of arable fields could have a beneficial role as prey for polyphagous arthropods which are useful in integrated pest management (IPM). Collembola are important prey organisms for many other soil inhabitants. They are preyed upon by mites (Acari), pseudoscorpions (Pseudoscorpionidae), staphylinid (Coleoptera, Staphylinidae) and carabid beetles (Coleoptera, Carabidae), Anthocoridae (Hemiptera, Heteroptera), young centipedes (Chilopoda), and other Collembola (e.g. Maclagan 1932a, 1932b, Christiansen 1964). A variety of studies have shown that Collembola are important prey organisms for stenophagous beetles (Ernsting 1977, Bauer 1985, Hintzpeter & Bauer 1986, Bauer & Pfeiffer 1991). In some species 70% of adult Collembola mortality has been attributed to predation (Ernsting & Joosse 1974), and the importance of Collembola as alternative prey to pest species for beneficial arthropods has been suggested by some researchers (e.g. Kielty *et al.* 1996, Sunderland *et al.* 1996, 1997). In conclusion, Collembola could be an important alternative prey source for supporting populations of beneficial arthropods when target pests are unavailable, since pests may only occur sporadically as a food source for beneficial predators (C. Mundy pers. comm.).

As Collembola can be an alternative prey source for beneficial insects, a potential disadvantage in their presence is that they may interfere with successful IPM regimes.

Mechanisms include distracting beneficial predators from feeding upon pest species (Chiverton & Sotherton 1991), and predation upon control agents (e.g. nematodes; Gilmore & Potter 1993).

Since most Collembola are at least facultative fungivores, they could be valuable for controlling pathogenic fungal infestations of crop plants (e.g. stem canker in potatoes - Lootsma & Scholte 1998). However, some pathogenic fungi are known to be toxic to Collembola (Sabatini & Innocenti 1995). Field trials using Collembola as biocontrol agents of fungal populations have not been successful (e.g. *Rhizoctonia solani* - Lartey *et al.* 1986, 1994, Rickerl 1986, Rickerl *et al.* 1989). Fungal grazing of mycorrhizae by Collembola has been suggested to have negative effects upon nutrient uptake by plants (e.g. McGonigle 1995). On balance Collembola are unlikely to be used as biological control agents with respect to their role in fungal population dynamics in the field.

1.3.3 Collembola as pests

There are many reports of Collembola as agricultural pests (e.g. *Lepidocyrtus* spp. and *Onychiurus* spp. - Ingram 1931; *Onychiurus* spp. - Getzin 1985; *Bourletiella hortensis* - Honma 1988; *Onychiurus* spp. - Heisler 1989; *Entomobrya unostrigata* - Greenslade 1995) particularly for *Sminthurus viridis* in Australia (Frogatt 1907, Maclagan 1932a, 1932b, Ireson 1993, Ireson & Webb 1996). Control measures for *S. viridis* have attempted using predatory mites (Ireson & Webb 1996). Feeding by *Onychiurus armatus* on sugar beet may cause yield losses in Europe (e.g. Gratwick 1992), but Sievers & Ulber (1990a) found that high Onychiurid populations did not negatively affect the emergence or growth of seedlings. Honma (1988) and Hurej *et al.* (1992) concluded that *Bourletiella hortensis* was not likely to

be an economically important pest on sugar beet. It may be concluded that some species of Collembola are economically important pests, but problems in European arable fields are mainly confined to outbreaks of *S. viridis* in Spain (Gimeno & Perdiguer 1995).

1.3.4 Conclusions

The evidence for the importance of Collembola in arable ecosystems is inconsistent. Their role as biocontrol agents is very doubtful, being largely unsubstantiated by experimental evidence. They appear to be serious pests only in southern Australian pastures. As alternative prey species they may distract beneficial organisms, but on the other hand they may have a positive role in helping to maintain high populations of beneficial invertebrates. More information is needed to clarify the potential economic value of Collembola in agriculture.

1.4 Effects of non-pesticide sources of disturbance in agroecosystems

Collembolan abundance in arable fields is affected by a variety of non-pesticide sources of disturbance. These factors can interact with pesticide effects and thus should be considered in conjunction. Factors which have been found to influence Collembola in arable fields include climate, in particular drought; cultivation effects including tillage and soil compaction; crop cover; and fertiliser applications. These factors could influence the vulnerability of different species to pesticides by altering their population abundance or distribution in arable fields.

1.4.1 Drought

In general Collembola breathe through their integument, which makes them prone to desiccation (e.g. Joosse & Groen 1970) and hence humidity and temperature are critical factors in their distribution. They lack a true respiratory tracheal system, although some Sminthuridae do have an internal tube-like air breathing system (e.g. Christiansen 1964, Ellis 1973). Collembola moult throughout their lives, which has an important excretory function since they lack Malpighian tubules. This physiological aspect of collembolan biology is likely to influence the degree of exposure to pesticides: firstly, having a thin and permeable integument which is frequently shed might make them vulnerable to absorbing pesticides directly through their cuticle; secondly, it may also make many species vulnerable to stress caused by drought and this may make individuals more likely to succumb to exposure to pollutants (Pedersen *et al.* 1997).

Although Collembola are generally considered to be vulnerable to desiccation (Joosse & Groen 1970, Verhoef 1981, Verhoef & van Selm 1983), there are species-specific differences with *S. viridis* and *E. multifasciata* being more resistant than *Tomocerus vulgaris, Isotoma viridis* and *Dicyrtoma minuta* (Davies 1928). Increases in summer droughts in northern Europe could thus have implications for the population dynamics of these organisms. The effects of potential climate change including drought were investigated by Masters *et al.* (1998a, 1999), who found that certain grassland species were favoured by dry conditions, specifically Symphypleona including *S. elegans*. Collembola can cope with the effects of drought in arable fields by behavioural or physiological means (Poinsot-Balaguer 1990). To avoid water loss, vulnerable species can form aggregations (Joosse & Groen 1970) or build 'chambers' (Massoud *et al.* 1968). Alternatively, species can avoid periods of drought by aestivating as desiccation-resistant eggs or adults (Greenslade 1981). The

avoidance of drought by aestivation or diapause has been studied in *S. viridis* (Maclagan 1932a), *Onychiurus meridiatus* (Argyropoulou & Stamou 1993) and *S. aureus* (Blancquaert *et al.* 1981). Temporal or spatial variations in climate could have implications for the exposure of Collembola to pesticides and subsequent recovery in arable fields because of these different avoidance strategies. Behavioural methods to avoid desiccation could reduce collembolan exposure to some (i.e. sprayed) pesticide applications. Physiological avoidance by drought-resistant eggs could affect sensitivity, since previous work has suggested that the eggs of some species are less sensitive to pesticides than juveniles or adults (Chernova *et al.* 1995). However the potential effects of drought on the majority of the Collembola of temperate arable fields remains unknown, but is relevant to the study of non-target pesticide effects since drought exposure is likely to alter collembolan community composition and hence the degree of exposure of different species to pesticides.

1.4.2 Cultivation

Collembola are exposed to harsh and variable environmental conditions by regular tillage of the soil, which destroys its natural stratification. Together with the cyclical removal of vegetation cover, these patterns of disturbance cause a reduction in the abundance and diversity of populations (Morris 1922, Edwards & Lofty 1969, 1975, Rickerl *et al.* 1989, Hendrix *et al.* 1986, Larink 1992). Soil compaction has been extensively studied and reported to be detrimental to Collembola, particularly euedaphic species (Heisler 1991, 1993, 1994a, 1994b, Heisler & Kaiser 1993, 1995, Schrader & Lingnau 1997). Different tillage regimes have been used to explain high numbers of Collembola found in organic cultivation (Moreby *et al.* 1994) and variation in numbers on different soil types (Kovac & Miklisova 1997) by

affecting microbial and fungal food resources (Heisler & Kaiser 1993). The use of reduced tillage and cover crops can enhance the accumulation of organic matter on the soil surface, preventing evaporation and thereby conserving soil moisture (see Locke & Bryson's 1997 review of tillage systems). The higher soil moisture and labile organic carbon improves conditions for microbial and fungal activity, and thereby provides an increased food supply for Collembola. However, tillage has also been reported to have no significant effects upon Collembola populations (Fromm *et al.* 1993a, 1993b, Diekkrugger & Röske 1995, Sabatini *et al.* 1997). Species-specific responses to tillage (e.g. see Gers 1982) and the spatial scales of different studies may explain the inconsistencies reported in the literature, which could also be due to the different types, timings and frequencies of tillage practices investigated.

1.4.3 Effects of fertilisers

The application of fertilisers as inorganic additions or as green manures has been reported to have positive effects on collembolan abundance. Manure applications were found to increase collembolan biomass and species diversity (Morris 1922, Christiansen 1964 and references therein, Tarba 1990, Filser 1995a) although collembolan responses may vary depending on the timing and application method (Sievers & Ulber 1990b). However, some species were found to be vulnerable to nitrogen fertilisers at high rates of application (Kopeszki 1993b, Trojanowski & Baluk 1993). One study has reported no differences in abundance between barley fields with and without nitrogen additions (Lagerlof & Andren 1991). This inconsistency may be due to the small spatial scale at which this study was made (40 m by 14 m plots) in which dispersal may have notably contributed to recovery. Spatial

scales are important in determining experimental results and thus should be considered in comparisons among studies (Weins 1989, Levin 1992).

1.4.4 Crop canopy type

Varied and often contradictory results have arisen from studies looking at the effects of vegetation cover on communities of Collembola. A more diverse arthropod fauna has been described in perennial than in annual crops (Purvis & Curry 1980) although contradictory results have also been reported (Rickerl *et al.* 1989). Contradictory results may have been found because some studies did not consider differences in the pesticide regimes for the different crops. Higher populations of Collembola have been reported in cereals, particularly winter barley, than in root crops (Jagers *et al.* 1988, Heisler & Kaiser 1995). Significant differences among a variety of different crop types have been reported and it has been suggested that crop cover is a more important determinant of population abundance than soil type (e.g. Fromm *et al.* 1993b, Diekkrugger & Röske 1995). However, effects of crop or vegetation cover on species composition were lacking in other studies (Wardle *et al.* 1993, Lagerlof & Andren 1991, Ponge 1993), and generally these studies have attributed a stronger influence to differences in soil type.

There are conflicting reports on the role of vegetation cover upon collembolan communities, and clearly more research is needed in this area to elucidate any patterns of abundance.

1.5 The effects of pesticides upon Collembola

Numerous laboratory and field investigations have been carried out to investigate the effects of pesticides on Collembola. Contradictory results are widespread and may be due to differences in the statistical techniques in the analysis or aspects of the scales of experiments and, in field studies, sources of recolonisation for recovery. The results of studies on fungicides, herbicides and insecticides are discussed in the following sections. Results for other pesticides used in the field such as mollusc pellets and bacterial insecticides are summarised in Appendix I. The factors determining the vulnerability of Collembola to pesticide applications in arable fields are discussed in section 1.6.

1.5.1 Effects of fungicides

The application of fungicides may affect Collembola both directly on contact or by ingestion, or indirectly by changes in food availability (see Appendix II). Collembola are polyphagous feeders (Macnamara 1924, Vegter 1983, Honma 1988, Shaw 1988, Lee & Widden 1996) but it is generally accepted that the majority of their intake consists of fungal spores and hyphae (Christiansen 1964, Bödvarsson 1970, McMillan 1975). Since the majority of Collembola feed on fungi, and use of fungicides is widespread in agriculture (on average four applications per hectare per season in UK arable fields; Thomas 1997), Collembola could be negatively affected by fungicide use indirectly due to the loss of their food resource.

Generally fungicides have been found to decrease population levels in the field (e.g. Sotherton *et al.* 1987, Frampton 1989, Kaluz *et al.* 1993, Filser 1994), although lethal effects have not always been observed in laboratory studies (e.g. Triadimenol - Frampton 1989)

suggesting that the mechanism of detrimental effects may be sublethal or indirect. The lack of effects in laboratory tests has particular implications for the certification of fungicides for use in farms. Potentially damaging indirect effects may not be detected by standard chemical certification testing. Laboratory tests representing the 'worst case scenario' may show a fungicide to have no detrimental effect, but when tested in the field the pesticide may affect population levels. For example, Propiconazole had no direct toxic effect on *I. viridis* in laboratory tests, but reduced populations in the field (Frampton 1989). This implies that laboratory testing may not adequately quantify the potential damage to field populations, a problem common to the testing of all pesticides.

1.5.2 Effects of herbicides

The effects of herbicides on collembolan populations have varied between studies with positive, negative and no effect being found (see Appendix III). Herbicide applications can have direct toxic effects (e.g. atrazine - Mola *et al.* 1987), or they may act indirectly to increase (e.g. atrazine - Moore *et al.* 1984, Mallow *et al.* 1985) or decrease (e.g. atrazine - Fratello *et al.* 1985, 1986) collembolan populations. It is noticeable that the same chemical can be reported to have both detrimental and positive effects on collembolan populations (e.g. atrazine and paraquat in Appendix II). Atrazine was found to have indirect detrimental effects on herbivorous Collembola by making the food repellent and thus leading to starvation (Subagja & Snider 1981). Positive effects could be due to an increase in fungal abundance following an increase in organic matter in the soil after herbicide application (e.g. Mallow *et al.* 1985).

The effects of herbicides can also be affected by soil cultivation techniques: for example under a low tillage regime organic matter is allowed to build up on the soil surface and this could provide shelter from direct herbicide exposure for Collembola (see Locke & Bryson 1997 and references therein). Thus pesticide effects cannot be realistically considered in isolation of other features in arable management. The longevity of herbicides, in common with other pesticides, is affected by pH and moisture and thus can vary according to the soil type encountered. Residues of atrazine and chlorsulphuron are known to build up with consecutive applications (Freemark & Boutin 1995 and references therein).

1.5.3 Effects of insecticides

Collembola have been found to be sensitive and vulnerable to many insecticides (see Appendix IV). They are especially vulnerable to organophosphorus compounds sprayed in the field: broad-spectrum organophosphorus insecticides such as dimethoate, parathion and chlorpyrifos which are moderately persistent in the field have been reported as highly toxic (e.g. Crommentuijn *et al.* 1995, Wiles & Frampton 1996) and found to have long-term detrimental effects upon field populations (e.g. Frampton & Çilgi 1992, Çilgi & Frampton 1994). Chlorinated hydrocarbons (no longer widely used in Europe) such as lindane which are highly persistent can also be highly toxic to Collembola (e.g. Thompson & Gore 1972) and can cause long-term negative effects in agricultural fields (e.g. van de Bund 1994, Gregoire-Wibo 1983), although DDT has been reported as not very toxic to Collembola (e.g. Lupetti *et al.* 1994). The toxicity of carbamates on Collembola has also been investigated (e.g. Getzin 1985). These insecticides, e.g. pirimicarb, carbofuran and carbaryl, have short persistence (see van Straalen & van Rijn 1998 and references therein). They have been reported as being toxic

to *Folsomia candida* (Tomlin 1975) and other Collembola (Martin 1976, 1978), and recommended for the control of pest *Onychiurus* spp. (Getzin 1985) and *S. viridis* (Bishop *et al.* 1998). However no long-term studies investigating carbamate use have found persistent reductions in abundance (e.g. Frampton 1997b). Collembola appear to be least sensitive to pyrethroids such as cypermethrin. Toxic effects have been reported for Collembola exposed to residues on freshly sprayed soils (e.g. Wiles & Frampton 1996), but again no long-term detrimental effects have been reported (e.g. Cole & Wilkinson 1985, Frampton 1997a, 1997b).

1.5.4 Long-term studies of pesticide effects

The results of long-term studies comparing different pesticide regimes and their effects on non-target organisms were summarised by Holland *et al.* (1994). Few studies investigated the effects of pesticides upon Collembola populations in detail. Long-term research at Boxworth in the UK (Greig-Smith *et al.* 1992) compared the effects of an intensive with a reduced pesticide regime on a variety of arthropods (Vickerman 1992). Generally Collembola were found to be more vulnerable to pesticides than Coleoptera or Acari with species-specific differences in abundance found between the pesticide regimes (Frampton *et al.* 1992). Some increases in abundance noted in the high input fields may have been due to a reduction in predation caused by pesticide applications.

Research carried out in the SCARAB (Seeking Confirmation About Results At Boxworth) project in the UK investigated the long-term effects of pesticides on Collembola (e.g. Frampton & Çilgi 1993, Çilgi *et al.* 1993, Frampton 1999). Some pesticides had long-lasting effects upon collembolan abundance, particularly of the genus *Lepidocyrtus*

(Frampton 1997b). However, long-term studies have frequently lacked replication. Hence although long-term studies have suggested that Collembola are more sensitive to pesticide use than many of the currently used indicators, more information is needed upon the scales of population and community variation in order to confirm these findings and develop appropriate monitoring schemes.

1.6 Ecological aspects determining the vulnerability of Collembola to pesticides in arable fields

The vulnerability of a species to pesticide indirect effects is a function of its innate sensitivity, the degree to which it is exposed, and its ability to recover from the pesticide (Brown 1986, 1988, van Straalen 1994, van Straalen & van Rijn 1998). Exposure is influenced by a combination of biotic and abiotic factors. Abiotic factors include aspects of a pesticide's application in the field, for example its formulation, persistence and bioavailability in different types of soils (e.g. Martikainen 1996), the timing of application and the degree of drift which occurs during application. The biotic factors determining exposure include the species' life history, diet, activity, spatial distribution and habitat preferences, as well as vegetation cover. Recovery is affected by a species' reproductive and dispersive capabilities (e.g. Burn 1992), the persistence of the pesticide, the area treated and availability of refuge habitats from which recovery can take place (Sherratt & Jepson 1993, Halley & Lawton 1996). Since this thesis is specifically addressing aspects of collembolan ecology, the biotic factors will be the focus of this review and abiotic factors will not be specifically addressed with respect to their effects on collembolan population dynamics.

1.6.1 Factors determining the exposure of Collembola to pesticides

Pesticides applied in the autumn and winter have a greater impact on arthropod populations than ones applied in the summer (Vickerman 1992). Carabid beetles, particularly *Bembidion obtusum* which has one generation a year and overwinters on the soil surface in fields, were vulnerable to broad-spectrum insecticide applications due to these aspects of their phenology (Burn 1992). A similarly detailed knowledge of collembolan life histories would be useful, since the exposure of Collembola to pesticide applications will also be determined by their spatial distribution, diet and life history characteristics.

Species differ in their preferred location down the soil profile (Takeda 1978, Usher 1969, 1970, Filser & Fromm 1995). Species on the soil surface are directly exposed to pesticide applications (higher doses than expected by a homogenous pesticide distribution are found at the soil / air interface - van Straalen 1994) although this varies according to the degree of shelter offered by different types of vegetation canopy. Collembola which are active in the crop could be exposed to higher dosages as pesticide deposition decreases down a crop, although this also varies between abaxial and adaxial leaf surfaces (Çilgi & Jepson 1992).

The spatial distribution of Collembola can also be altered by diel patterns of activity. Pesticide applications coinciding with peak collembolan activity (morning and late afternoon and evening - Desender *et al.* 1984, Frampton 1989) may cause maximum direct exposure. Active avoidance of pesticide residues may also alter collembolan exposure. Some species of Collembola actively avoid herbicides (e.g. Eijsackers 1975, 1978, Subagja & Snider 1981) and insecticides (Petersen & Gjelstrup 1998).

Collembolan abundance is extremely variable between seasons in most ecosystems (e.g. in forest ecosystems - Moldenke & Thies 1996a, 1996b; grazed grasslands -

Argyropoulou *et al.* 1994; grass tussocks - Hertzberg *et al.* 1994; and agricultural fields - Diekrugger & Röske 1995). These seasonal fluctuations are more noticeable in epigeal than euedaphic species, since the former are more exposed to climatic fluctuations especially in temperature and humidity (Christiansen 1964, Filser 1995b). Species within families such as the Sminthuridae and Entomobryidae, which are largely surface-dwellers, might therefore be expected to exhibit different seasonal patterns from subterranean species which inhabit a less variable environment. Relatively few studies have investigated the annual phenologies of common agricultural collembolan species in detail (but see Diekkrugger & Röske 1995 for temporal variability in *Isotoma notabilis,* and Maclagan 1932a, 1932b for the phenology of *S. viridis*, Blancquaert *et al.* 1981 for *Sphaeridia pumilis*). Populations of epigeal Collembola peak in summer and are minimal during winter in temperate areas (Dhillon & Gibson 1962), whilst in Mediterranean systems populations are extremely low during the dry summers (Stamou *et al.* 1993). Further information on individual species phenologies is required in order to interpret mechanisms of observed pesticide effects, including the poor ability of some species to recover (e.g. Frampton 1999). It is necessary to establish which species are present in arable fields at the times when different pesticides are applied. Since overwintering strategies have been previously suggested to influence the exposure of predatory arthropods to pesticides (Burn 1992), collembolan presence in temperate arable fields during winter was investigated in the present study (Chapter 2).

1.6.2 Mechanisms determining the recovery of Collembola

The recovery potential of collembolan populations following a pesticide perturbation depends in part on the persistence of the chemical in the environment (van Straalen & van

Rijn 1998); the persistence of pesticides was briefly discussed in section 1.5 on pesticide effects. Spatial parameters which include a species' ability to recover, the presence of source populations and dispersal ability, also influence recovery and will be discussed in the following paragraphs.

The distribution of refuges in the arable landscape has been identified as being imperative in the recovery potential of arthropods in arable fields (Sherratt & Jepson 1993), with hedgerows and grass banks being particularly important (Forman & Baudry 1992, Dennis & Fry 1992, Dennis *et al.* 1994, Burel 1996). Since collembolan dispersal is poorly understood in agricultural habitats, it is not clear whether habitat features such as hedgerows or 'beetle-banks' provide sources of dispersal for either or both of epigeal and euedaphic species. If species are poorly dispersive, and such habitats are important sources of recruitment, then recovery is unlikely to occur quickly. However no information on the availability or use of refuges, or on the role of hedgerows as refugia, is available for Collembola. The role of hedgerows as sources of collembolan colonisation of arable fields (e.g. after pesticide use or tillage disturbance) was therefore investigated in the current work (Chapter 3).

Starvation, which is encountered seasonally in the field either due to fungicide applications or to seasonal factors in food distribution, has been found to lead to a cessation in moulting and egg production, thereby inhibiting the capacity for population recovery (Joosse 1973, Joosse & Testerink 1977, Testerink 1983). Surface-dwelling Collembola were found to be better adapted to food scarcity than euedaphic species (Joosse 1973, Joosse & Testerink 1977, Testerink 1983). Life history and reproductive strategies have several implications for determining the recovery of species. Species such as the parthenogenetic *Folsomia candida* with short lifecycles and high reproductive potential can recover quickly. The rate of reproduction determines a species capacity to recover and is affected by several

parameters including food quality, temperature, humidity, population density, pH, and salinity (e.g. Maclagan 1932a, Christiansen 1964, Joosse *et al.* 1973, Hutson 1978, van Amelsvoort & Usher 1989). More information on species' reproductive capacities is necessary to evaluate the potential of different species to recover from pesticide effects at different times of the year.

Recovery of populations can also occur *in situ* by the survival of individuals in the field despite the pesticide application. The ability of eggs to withstand pesticide applications (Chernova *et al.* 1995) could provide a source for recovery within fields. This source of recruitment could be of particular importance if Collembola have limited rates of dispersal. In the current work, the presence of collembolan eggs in arable soils is reported in Chapters 2 and 4.

The rate of recovery following depletion of a population is dependent on both the geographical extent and frequency of pesticide use and the source of potential immigrants as well as the persistence of the pesticide in question (van Straalen & van Rijn 1998). Dispersal rates may therefore be of paramount importance in recovery, and local extinctions are likely to be short-lived in organisms with high dispersal rates such as linyphiid spiders (Halley & Lawton 1996). Previous work has suggested that the invertebrate fauna of arable fields contains organisms which are pre-adapted to the frequent patterns of disturbance typical of arable agroecosystems, in which a species' propensity for dispersal is an evolutionary stable strategy to maximize fitness in a landscape of frequent disturbance (Halley *et al.* 1996).

The dispersal ability of collembolan species in agricultural fields at landscape scales (i.e. between fields) is largely unknown and has seldom been studied (e.g. Mebes & Filser 1997). Investigations into recolonisation can provide some information about dispersal ability in other habitats. Species-specific recolonisation rates have been found (Parsons & Parkinson

1986) which suggested that the dispersal ability of some Collembola lies between that of arachnids, and that of the Formicidae and Isopoda (Judd & Mason 1995).

On a worldwide scale Collembola appear able to disperse widely (see e.g. Christiansen & Culver 1968, 1969, Christiansen & Bellinger 1995 for general reviews on biogeography) by passive and active mechanisms. Passive mechanisms include wind, phoresy and water runoff, but no conclusive empirical evidence has been presented (Baweja 1939, Glick 1939, Freeman 1945, 1952, Delamare-Debouteville 1951, Gresitt *et al.* 1960, Christiansen 1964, Joosse 1966, Paclt 1967, Rapaport 1969, Purvis & Curry 1980, Usher 1985, Blackith & Disney 1988, Witteveen & Joosse 1988, Hertzberg *et al.* 1994, Siepel 1994, Hopkin 1997a). Dormant eggs which remain viable through a period of flooding could enable some species to be dispersed by water (Tamm 1986a, Gauer 1997). Active dispersal can occur by mass migrations (Lyford 1975, Leinaas 1981, 1983, Hägvar 1995). Local scales of active dispersal have been investigated in the laboratory for mainly euedaphic species (Christiansen 1970, Joosse & Verhoef 1974, Johnson & Wellington 1983, Faber & Joosse 1993, Bengtsson *et al.* 1994a, Fabian & Petersen 1994) and suggest very short dispersal distances (e.g. 1.3 cm per day - Sjögren 1997; see also Bengtsson *et al.* 1988, 1993, 1994b). Thus, this directional dispersal among euedaphic species seems unlikely to be of importance for recovery at landscape scales, although the situation for epigeal species is not known.

In general the studies of recolonisation suggest that there are species of Collembola which are generalists, good colonisers and hence good dispersers, able to withstand disturbed habitats and reproduce quickly (i.e. they have 'r' selected life history strategies - Pianka 1970). The species present in agricultural fields are likely to be 'r' life strategists, as they are pre-adapted to the repetitive cycles of disturbance caused by management which maintain fields as early successional habitats (Wissinger 1997). More information on collembolan dispersal at landscape scales, especially on species-specific differences between epigeal,

hemiedaphic and euedaphic species, would be helpful to explain observed patterns in recovery in agricultural fields following detrimental pesticide applications.

1.7 Using Collembola for monitoring pesticide non-target effects

Collembola have been proposed as reliable indicator species for investigating pesticide non-target effects both in laboratory and field studies because of their sensitivity and vulnerability to pesticides. There is a wealth of information on the use of Collembola as test organisms in laboratory studies and this shall be concisely reviewed here. Interest in the use of Collembola as ecological monitors in the field is growing and is briefly summarised in the following section.

1.7.1 The use of Collembola in laboratory studies

Ronday & Houx (1996) compared the suitability of seven species of soil-inhabiting invertebrates for testing the toxicity of pesticides in soil-pore water and found that the most suitable organism in terms of sensitivity, amenability and reproducibility of results was the euedaphic collembolan *Folsomia candida*. *F. candida* is widely available and easily cultured, and has been increasingly used routinely in laboratory tests; it is a recommended standard test organism (Riepert & Kula 1996, Wiles & Krogh 1998). Other species have been reared successfully in the laboratory and used in ecotoxicological tests (e.g. *I. viridis* and *F. fimetaria* - Wiles & Krogh 1998). Some experiments have used individuals collected in the

field (e.g. Wiles & Frampton 1996), although it is less easy to standardise age, sex and size in these cases.

It is important to note the limitations of using a single species, i.e. *F. candida,* as a standard test organism. This constraint was expressed by Hopkin (1997a) as:

> "Choosing the parthenogenic species *Folsomia candida* as representative of all Collembola (the 'standard springtail') is about as ecologically sound as choosing a mole as a 'typical' mammal."

Clearly not all the species present in arable fields will respond in the same way to pesticide applications, in particular as *F. candida* in the field is a subterranean species and as such will differ in exposure and recovery rates from epigeal species (see section 1.6.1 and 1.6.2). Results from *F. candida* may be irrelevant to agricultural situations since this species is rare in many arable fields (Rusek 1995). Furthermore it is important to note that experimental conditions may determine the outcome of laboratory studies on population dynamics. For example, heterogeneous conditions in a three-dimensional test area have led to a greater stability in *F. candida* populations than in a simple two-dimensional experiment, possibly due to the presence of refuges for eggs and fungus (Leonard & Anderson 1991). A standardised collembolan testing scheme has been developed for pesticides (Riepert 1991, Riepert & Kula 1996).

Tiered systems for testing the effects of chemicals used in arable farmland were recently evaluated, and criteria for choosing suitable test soil organisms were suggested (Rombke *et al.* 1996). The criteria were set according to ecological, ecotoxicological and practicability parameters. The ecological and ecotoxicological criteria are that the organism: (1) has an important role in the soil ecosystem; (2) has a wide geographic range and inhabits a

range of soil types; (3) comes into close contact with the chemical; and (4) has a moderate and consistent sensitivity to a wide range of chemicals. The criteria for practicability were that the test organism should be easy to handle and culture, have a high reproductive rate and short generation times, and should be easy to standardise (e.g. sex, age, size). In addition, the authors suggested that suitable organisms should also fulfil the criteria of: (1) availability for testing several different stressors; (2) enabling various trophic and taxonomic levels to be considered; and (3) providing results which are useful for an overall assessment scheme of the potential effects of the pesticide in the environment. Collembola appear to fulfil the majority of these criteria and hence could be suitable test organisms, however more information is required on the amenability of species other than *F. candida*.

In conclusion, the use of Collembola as standard laboratory test species is becoming widely accepted, but it is desirable to find out whether the results of these laboratory-based studies, usually carried out on a single species, are corroborated by studies of pesticide non-target effects in the field.

1.7.2 The potential of Collembola as bioindicators in arable fields

Several studies have suggested that Collembola may be reliable indicators of disturbance such as pollution to ecosystems. Collembola have been proposed as bioindicators of heavy metal pollution (Lubben 1989, Kopeszki 1992a, Greenslade & Majer 1993), rock salt pollution (Rösgen *et al.* 1993), soil acidification (Kopeszki 1992b, 1993a, van Straalen and Verhoef 1997) and agricultural impact (e.g. tillage - Gers 1982, Gers & Izarra 1983; intensive farming - Filser 1995b).

The sensitivity of certain species of Collembola to pesticides in arable fields has been demonstrated in both long-term and short-term studies, both in the laboratory and the field (e.g. Frampton 1994, Ronday & Houx 1996, Martikainen 1996, Steiner *et al.* 1986). Collembola fulfil many of the requirements for biological indication (see section 6.3) and as such could provide an important monitoring tool in agricultural ecosystems. However, much of the ecology of Collembola in relation to the effects of pesticide use in arable fields is still poorly known. The variation in collembolan abundance among arable fields exposed to different farming systems has been addressed in this study (see Chapter 5). More information on the ecology of collembolan communities, particularly with regard to their overwintering and dispersal strategies and sources of recovery, is essential in order to understand the effects of pesticides in the long and short-term and the mechanisms of recovery from such perturbations (see Chapters 2, 3).

1.8 Objectives of this thesis

Collembola are widespread and appear to have important roles in maintaining soil structure, decomposition processes and as prey for beneficial arthropods. Many epigeal collembolan species are vulnerable to effects of pesticides, and are generally more sensitive than many predatory species currently used to detect non-target pesticide (Vickerman 1992, Hancock *et al* 1995). Collembola could therefore be considered as potentially good candidates for ecological monitoring. However, knowledge about collembolan ecology in arable fields is limited and this precludes the choice of appropriate species for monitoring non-target, detrimental pesticide effects.

The overall aim of this thesis was to increase the current knowledge of collembolan ecology in agricultural landscapes in relation to pesticide use. Specific aims were to investigate aspects of collembolan ecology likely to affect: (1) exposure; (2) recovery; (3) the responses of populations and communities to different farming systems (of which pesticide use was a component); and (4) the potential of different species as ecological indicators. This thesis focuses on epigeal species of Collembola since previous work has suggested that they are vulnerable to pesticide applications (e.g. Frampton 1988, 1989, Frampton *et al.* 1992).

In Chapter 2 basic information is presented on the sampling and ecology of collembolan populations in arable fields. An appropriate sampling scheme is developed for estimation of the size and variability of field populations. Information is also given on the spatial and temporal distribution of collembolan populations with respect to crop types, crop cover and refugia (e.g. hedgerows). These findings contributed to the development of the hypotheses investigated in Chapters 3, 4 and 5.

A study of the role of hedgerows as refuges or population sources for recolonisation of fields after disturbance by tillage is reported in Chapter 3. This work employed repeated sampling in a cereal field at different distances from a hedgerow in areas with and without exclusion barriers which were placed so as to prevent collembolan emigration from the hedgerow.

The presence of aestivating or diapausing eggs in field soil, which could influence both exposure to pesticides and subsequent population recovery, is described in Chapter 4. This work was carried out in order to assess the potential of eggs as sources for recovery after overwintering and after periods of drought.

The presence and abundance of Collembola in fields of organic, integrated and conventional winter wheat are reported in Chapter 5 at a variety of spatial scales (field to region) to provide information on the vulnerability of individual species or species

assemblages to different farm management regimes. The implications of the results of this work for the reliability of Collembola as indicators of farming system are discussed.

To conclude, the information learnt about collembolan ecology in previous chapters is reviewed in Chapter 6. The limitations of this study, the need for further investigation into collembolan dispersal at landscape levels, and the potential of Collembola as ecological monitors of non-target pesticide effects are discussed in the light of these findings.

2. Temporal and spatial patterns in the population dynamics of epigeal Collembola: the importance of hedgerow proximity and crop type.

2.1 Summary

1. The population dynamics of Collembola in two spring-sown crops, spring barley and vining peas, were investigated with respect to the importance of crop type and hedgerow proximity.

2. The variation in collembolan abundance among samples was investigated and suitable sampling intensities were determined to monitor collembolan field populations.

3. The spatial distribution of the collembolan fauna was investigated in relation to distance from the field boundary. Some species were associated with the edges whereas others were found both in the edges and the middle of fields.

4. Temporal changes in the spatial distribution indicated that hedges may be used as overwintering refugia by some species of Collembola; other species appeared to overwinter as either adults or eggs in the middle of fields.

5. The temporal occurrence of population peaks demonstrated that different species of Collembola showed peaks at different times in the year, and also displayed high variation in abundance over time.

6. There were clear differences both in population dynamics and community composition between the two crop types, in response to the different canopy structures and management techniques.

7. The initial results of this study were presented at the IX International Colloquium on Apterygota, Dublin 1996, and were published in Pedobiologia 41, 80-84, 1997.

2.2 Introduction

Long-term studies such as the Boxworth Project (Vickerman 1992), which monitored the effects of different pesticide regimes on farmland arthropods, suggested that the spatial and temporal occurrence of species could determine their exposure and vulnerability to pesticide use. Results for predatory arthropods indicated that phenology and dispersal ability were major determinants of the severity and persistence of pesticide effects, with poorly dispersive species that overwintered in the field being particularly vulnerable (Burn 1992). Very little comparable information exists for epigeal Collembola, and it was therefore of interest to investigate the dynamics of collembolan populations present over a growing season in arable fields.

The importance of hedgerows as reserves for the predator fauna of arable farmland has been studied in detail (Sotherton 1984, 1985) but few studies have investigated collembolan abundance in hedgerows (e.g. Pollard 1968a, 1968b). The presence of source populations is imperative for the recovery of populations following a pesticide application, and the rate of this recovery will be determined by the dispersal ability of the organisms being considered. The dispersal ability of Collembola in arable habitats is poorly known, although studies of recovery from other sources of disturbance such as fire or toxic metal pollution suggest that they are intermediate in recovery ability between Arachnida, which are highly mobile, and Formicidae and Isopoda (e.g. Judd & Mason 1995). The spatial and temporal aspects of recovery are important when considering pesticide effects in agroecosystems (see Chapter 1). This study investigated differences in population recovery rate after spring cultivation, between field edges bordering a hedgerow and field centres.

The type of crop cover in arable fields is also of importance for two major reasons: firstly, it affects the microclimatic conditions on the soil surface, improving moisture retention when a dense canopy is present; this is of importance to the humidity-sensitive epigeal Collembola (section 1.4.1). Secondly, the type and density of the canopy will also affect the amount of pesticide spray which epigeal species will be exposed to. This was demonstrated by Wiles and Frampton (1996) who compared collembolan exposure to insecticide residues under no crop cover, and under a mature wheat canopy. As expected, exposure of species on the soil surface was greater when crop cover was missing. This study compared two spring-sown crops, vining peas and spring barley, in order to compare the effects of these two very different canopy types upon the epigeal Collembola population.

The aims of this work were to investigate for two spring-sown crops, spring barley and vining peas: (1) the species composition of the collembolan fauna in relation to distance from the field boundary; (2) whether any species overwintered in the field; (3) the temporal and spatial occurrence of population peaks; (4) the difference in population dynamics and community composition between the two crop types; (5) the presence of specific species which, due to their ecology, could be vulnerable to winter or early spring pesticide applications. I also investigated the variation among samples of collembolan catch in order to determine appropriate sampling schedules for Collembola for the rest of the study.

2.3 Methods

2.3.1 Sampling Collembola in arable ecosystems

Methods for sampling Collembola in the field comprise soil cores from which Collembola are extracted using Tullgren funnels (e.g. see Grossman 1988, Greenslade 1973, 1974, 1978), pitfall trapping (e.g. Joosse 1965, Mebes & Filser 1997), sticky traps (Taverner *et al.* 1996), suction sampling (Johnson *et al.* 1957, Dietrick *et al.* 1961, Macleod *et al.* 1994, Stewart & Wright 1995) and surface searching (e.g. see Murphy 1960, Greenslade 1982). Several studies have compared the efficiencies of pitfall traps, sweep-netting and suction sampling (e.g. se Johnson *et al.* 1957, Turnbull & Nichols 1966, Purvis & Curry 1980, Berbiers *et al.* 1989, Mommertz *et al.* 1996). It has generally been concluded that suction sampling is the most efficient method for sampling epigeal species of Collembola. Frampton (1989, 1994) recommended a combination of suction and pitfall sampling. The major disadvantage associated with suction sampling is the need for dry weather, otherwise the equipment becomes very inefficient. I chose to use suction sampling since this technique has been demonstrated to be efficient and reliable, and used an adapted leaf blower (Ryobi RSV3100, available from Ryobi Lawn & Garden UK Ltd., Gloucestershire, UK). This suction sampling involved a minimum of crop disturbance and the sampling effort could be standardised to sample equally sized areas for the same amounts of time in different fields. Differences in catch due to diel patterns in abundance on the soil surface and vegetation were avoided by carrying out all sampling between 10:30 and 14:00 BST in all investigations.

2.3.2 Justification of sampling regimes

Frampton (1989, 1994) previously investigated the number of samples required to estimate collembolan field populations. However since a different suction sampling technique was used ('D-vac') it was necessary to verify whether a similar number of samples would be required using a Ryobi sampler. Many collembolan species form aggregations (e.g. see Joosse 1970, 1971, Verhoef & van Selm 1983), it is possible that limited sampling can produce over- or under-estimates of field populations and hence of pesticide effects. It is thus necessary to establish the amount of sampling, or sample area, required to get a reliable estimate of population abundance. Taylor (1961) developed a power law to describe the relationship between the variance and mean for clumped populations in which the variance is greater than, and it varies in proportion to, the mean as is the case for Collembola. Finch *et al.* (1978) combined Taylor's power law with an equation developed by Mukherji & Harcourt (1970) to estimate the required number of samples to describe a population with a given sampling precision, giving the equation:

$$\ln N = (\ln a - \ln p) - (2-b)\ln m \qquad (2.1)$$

where N the number of samples required, 'a' a sampling factor; 'm' is the observed mean (calculated from 4 samples in this study), 'b' a constant depending on the specific species and environmental conditions in which samples were taken; and 'p' is the sampling precision required. For Collembola a sampling precision of 20% has been previously deemed acceptable due to the very high heterogeneity found between samples (Frampton 1989).

This technique was used upon a set of between 15 and 17 sample means in order to determine the number of samples required to reliably estimate the collembolan abundance in a field. Suction samples were taken in arable fields in southern England using a Ryobi, and *S. elegans, S. viridis, I. viridis, I. notabilis, Isotomurus* spp., *E. multifasciata* and *Lepidocyrtus* spp. were then identified and counted in each sample. The species identified comprised those described as suitable for biological monitoring by Frampton (1994).

The results of regressions of mean against variance are shown in Table 2.1. As can be seen from the probability and R^2 values, the linear regression lines accurately described the relationship of the mean to the variance after transformation. Using equation (2.1) above, this data was then used to estimate the required number of samples to estimate abundance in the field; the results are shown in Table 2.2.

Table 2.1. Results of a regression of the natural-log transformed mean against the variance for a range of common field-dwelling Collembola.

Species	Regression equation $\ln S^2 = \ln a + b \ln m$	Significance ***= $P < 0.001$	R^2	Range of means
Lepidocyrtus spp.	$\ln S^2 = \ln 1.56 + 0.42 \ln m$	$F_{1,15} = 35.4$***	0.70	13.5-288
S. elegans	$\ln S^2 = \ln 0.23 + 0.60 \ln m$	$F_{1,14} = 80.7$***	0.85	1.3-195.5
S. viridis	$\ln S^2 = \ln 0.22 + 0.61 \ln m$	$F_{1,15} = 203.4$***	0.93	0.5-186.8
Isotomurus spp.	$\ln S^2 = \ln 0.37 + 0.69 \ln m$	$F_{1,13} = 73.2$***	0.86	0.1-63.5
I. viridis	$\ln S^2 = \ln 0.56 + 0.58 \ln m$	$F_{1,15} = 116.1$***	0.89	1.8-187.3
E. multifasciata	$\ln S^2 = \ln 0.24 + 0.59 \ln m$	$F_{1,13} = 88.0$***	0.87	0.5-41.8
I. notabilis	$\ln S^2 = \ln 0.56 + 0.50 \ln m$	$F_{1,14} = 211.3$***	0.94	0.3-175.3

Table 2.2. Number of samples required to estimate the field population mean in Ryobi catches of Collembola.

Species	Observed mean ±SE	Observed range of means	Number of samples required if the mean number per sample is:				
			1.0	2.0	5.0	10.0	50.0
Lepidocyrtus spp.	116.1±12.6	13.5-288.0	4097	11	2	1	<1
S. elegans	68.1±8.1	1.3-195.5	3147	12	3	1	<1
S. viridis	39.2±6.4	0.5-186.8	3127	12	3	1	<1
Isotomurus spp.	19.2±3.1	0.1-63.5	3634	15	4	2	<1
I. viridis	45.6±6.9	1.8-187.3	4385	16	4	2	<1
E. multifasciata	15.6±2.1	0.5-41.8	3185	12	3	1	<1
I. notabilis	57.3±9.0	0.3-175.3	4373	15	4	1	<1

2.3.3 The experimental site

The study fields belonged to The Manydown Company, Wootton St Lawrence, Hampshire, UK (51º 16' N, 1º 10' W). The eight fields were located on well-drained calcareous soils, ranging in size from 50 to 100 hectares, and were selected in spring 1996 to be homogenous in terms of soil type and cropping history. All the fields had been left as undisturbed soil over the winter, and had at least one side of continuous mature hedgerow. Four fields were planted with spring barley cv. Chariot, on 16-17 March; vining peas (cvs Vada and Sherborne) were planted in the remaining four fields on 1-4 May. Fields were subject to current farm practice management and had the following chemical inputs (H= herbicide; F= fungicide): Spring barley received bromoxynil + ioxynil (H), mecoprop (H), metsulfuron-methyl (H), carbendazim (F) on 14 May, flusilazole (F) on 26 May. Vining peas

received: glyphosate (H), simazine and trietazine (H), terbuthylazine + terbutryn (H) between 26-29 March.

Suction sampling began in all eight fields on 18 March. Four sampling points were placed 20 m apart and 2 m into the field, along the edge adjoining the hedgerow and over 40 m from the nearest other edges. Four sampling points were similarly located a further 50 m into each field. Suction samples were taken at each point using a Ryobi adapted as described in Stewart & Wright (1995). Each sample was taken by holding the suction tube (diameter 17 cm, height 1m) for 10 seconds in 5 random positions within 1 m^2 at each site, representing a sampling area of 0.454 m^2. Samples were taken every 3-4 weeks, whenever the weather was dry enough for sampling to take place, between 10:30 and 14:00 BST. They were frozen for storage and later cleaned using flotation in water.

2.3.4 Species identification

The Collembola were stored in 80% methylated spirit, and examined under a binocular microscope; specimens difficult to identify were mounted and examined further using a compound light microscope. Species were identified with the aid of Christiansen & Bellinger (1980, 1998), Fjellberg (1980) and Stach (1947, 1956, 1963). Entomobyrid species *Lepidocyrtus* spp. and *Isotomurus* spp. were not separated due to their problematic identification.

2.3.5 Choice of diversity index

Shannon-Wiener diversity indices were used to compare community composition and equitability between the two crop types and positions in fields. The relative merits of diversity indices have been discussed (e.g. Magurran 1988, Cousins 1991) and their major limitation is that they are unreliable for comparing diversity between different habitat types. This may be problematic in the current study; however it is debatable whether the two crops represent different habitats. In addition, Shannon-Wiener was chosen due to its amenability for use in parametric statistical analysis. If the Shannon-Wiener index is calculated from a number of samples, the index can be normally distributed (Magurran 1988). This indeed was the case for the results from this experiment, which meant that parametric statistics could be used to analyse the differences in community diversities between the different treatments.

2.3.6 Statistical analysis

A 2-way crossed ANOVA design was used to compare overall differences in species counts and diversity data among position in the field (edge or middle, a fixed factor) and crop type (peas or barley, a fixed factor). Repeated Measures ANOVA was used to compare the effects of position in the field (a fixed factor) and crop type (a fixed factor) upon the counts of individual species of Collembola, total counts for Symphypleona and Arthropleona, and diversity indices on successive dates. Prior to analysis the abundance data were transformed using $\log_{10}$; all the data were tested using the F_{max} test and the Levene test for homogeneity of variance, and the Tukey test for normal distribution to ensure that the assumptions of

ANOVA were met. The Mauchly sphericity test for homogeneity of covariance was carried out as the specific requirement for Repeated Measures ANOVA (Kinnear & Gray 1994); if this proved significant the Greenhouse-Geisser epsilon correction factor was used to adjust the degrees of freedom. All calculations were carried out using SPSS (©SPSS 1989-1997). Where population differences between individual fields were not significant it was considered valid to treat the fields as replicates of the crop and position treatments.

2.4 Results

2.4.1 Sampling scheme

The results for the seven common species considered above suggested that in most cases two samples would suffice to estimate their field abundance, except when species are present only in very low numbers. Four samples were chosen to estimate abundance but allow a margin for errors caused by lower catches than average in some samples. Four samples were also a practical number to work with from the point of view of sorting and identification purposes in order to minimise these time-consuming and laborious processes. Hence four replicates has been used as a standard throughout the rest of this thesis.

2.4.2 Temporal population patterns

Changes in species diversity were examined using the Shannon-Wiener index. Species diversity changed significantly over time ($F_{6,96} = 5.66$, $P < 0.001$), and a significant interaction between crop type and date ($F_{6,96} = 5.01$, $P < 0.001$; see Fig. 2.1), probably due to

the importance of sowing date on the development of the community in the two different crops. Differences between the two positions (field edge, centre) were also significant overall ($F_{1,16} = 19.69$, $P < 0.001$; see Fig. 2.2) and there was no time interaction. Thus the different communities in the edges and the middle of fields remained distinct throughout the crop's development. There was consistently a greater number of species in the field edges, although no clear pattern in the number of species in any of the treatments (crop type or field position) emerged over time. Results from March to August provided information on the presence and abundance of Collembola populations in the spring-sown crops.

The most common species encountered were: *Sminthurinus elegans* Fitch, *Sminthurus viridis* L., *Jeannenotia stachi* Jeannenot (synonymous to *Stenacidia violaceus* Reuter), *Bourletiella hortensis* Fitch, *Isotoma viridis* Bourlet, *Lepidocyrtus* spp., *Isotomurus* spp., *I. notabilis*, and *Entomobrya multifasciata* Tullberg. All were found in both crops and both field locations. The patterns of change in the community composition over time are shown in Figs. 2.3 to 2.7. The total abundance of Collembola changed significantly over time ($F_{4,52} = 11.8$, $P < 0.001$) and was dominated throughout by the symphypleonids ($F_{1,27} = 11.9$, $P < 0.001$).

Figure 2.1 Effects of crop type upon the Shannon-Wiener diversity index over time. Barley was planted on the 11.4.96; peas were planted on the 1-4.5.96.

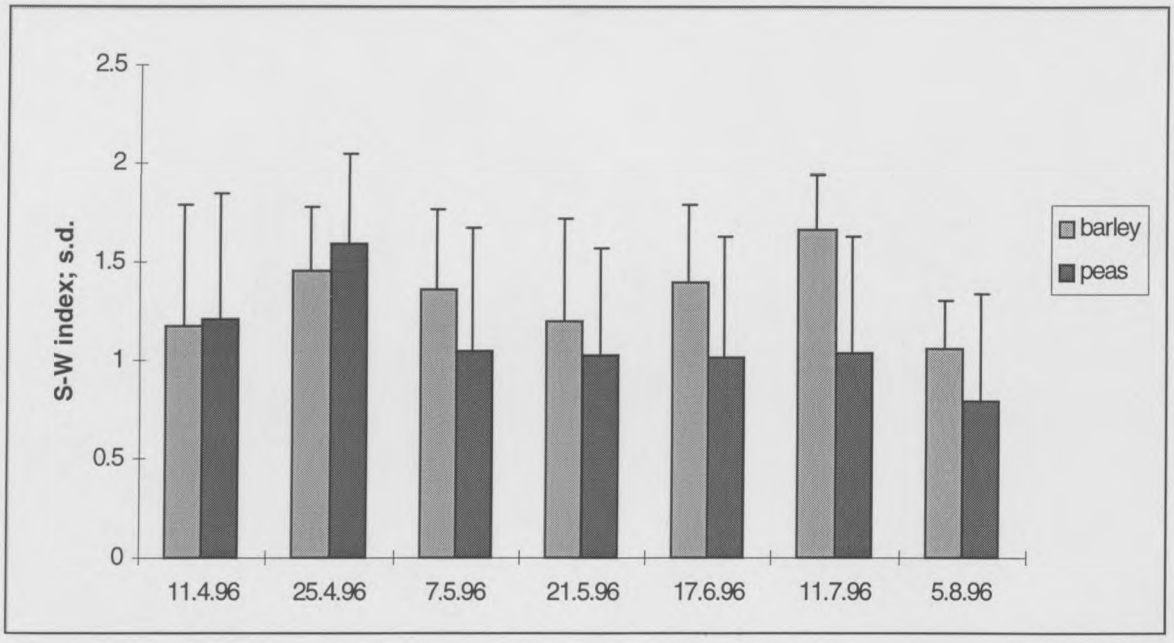


Figure 2.2 Effects of sampling position on the Shannon-Wiener diversity index over time.

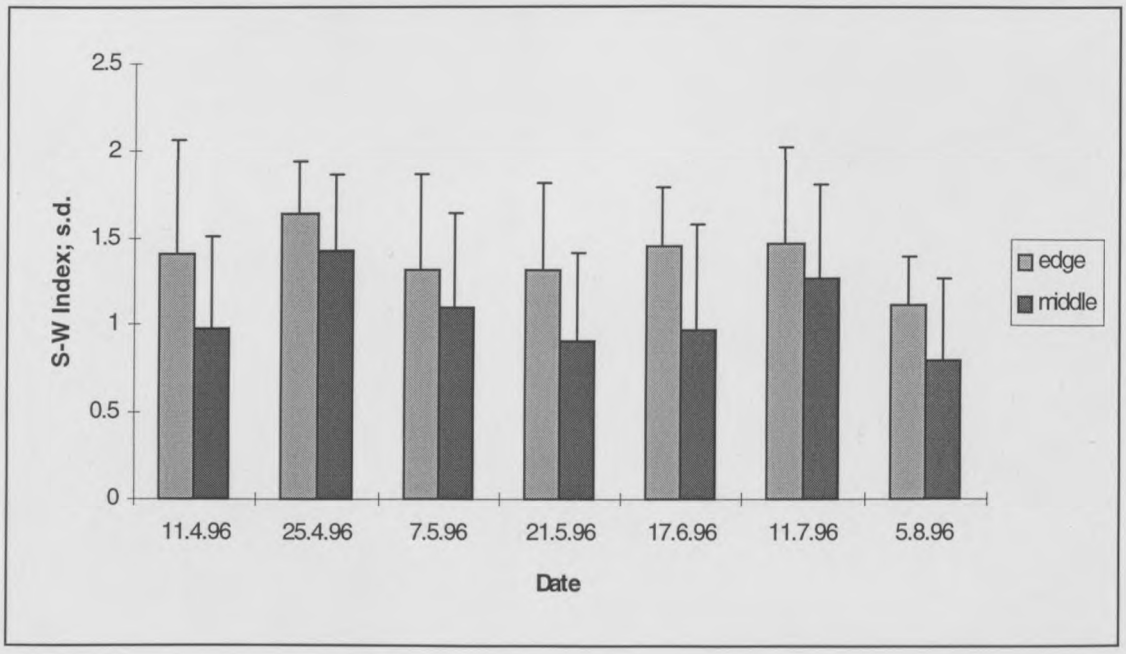


Figure 2.3 Species composition at the edges of barley fields over the growing season.

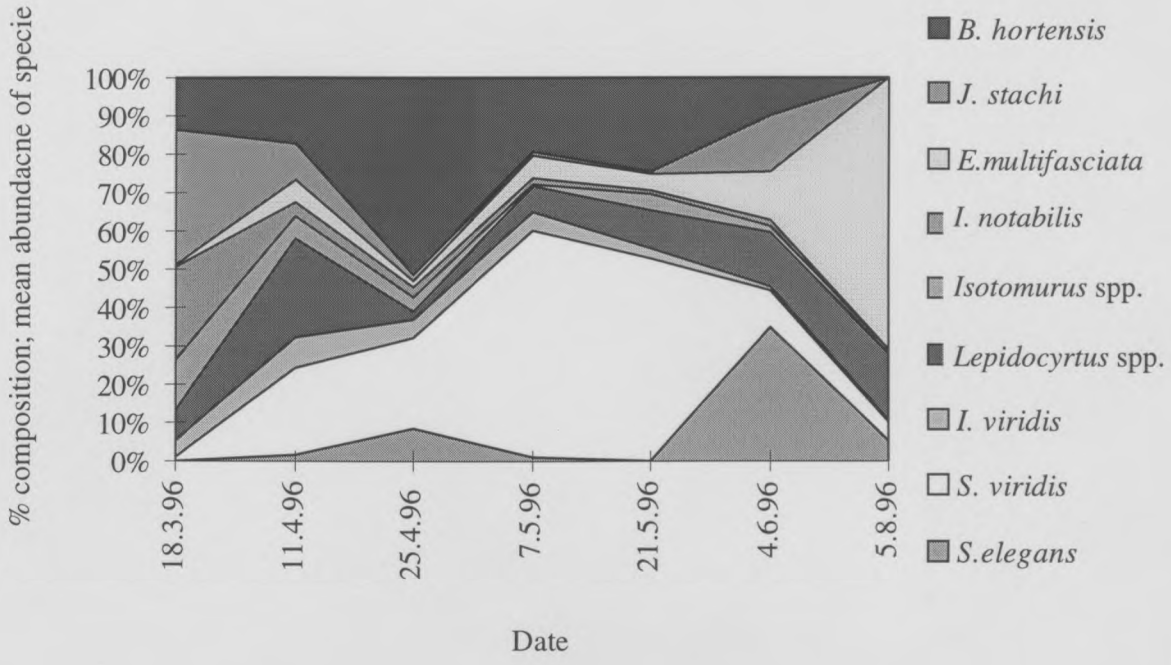


Figure 2.4 Species composition on the edges of pea fields over the growing season.

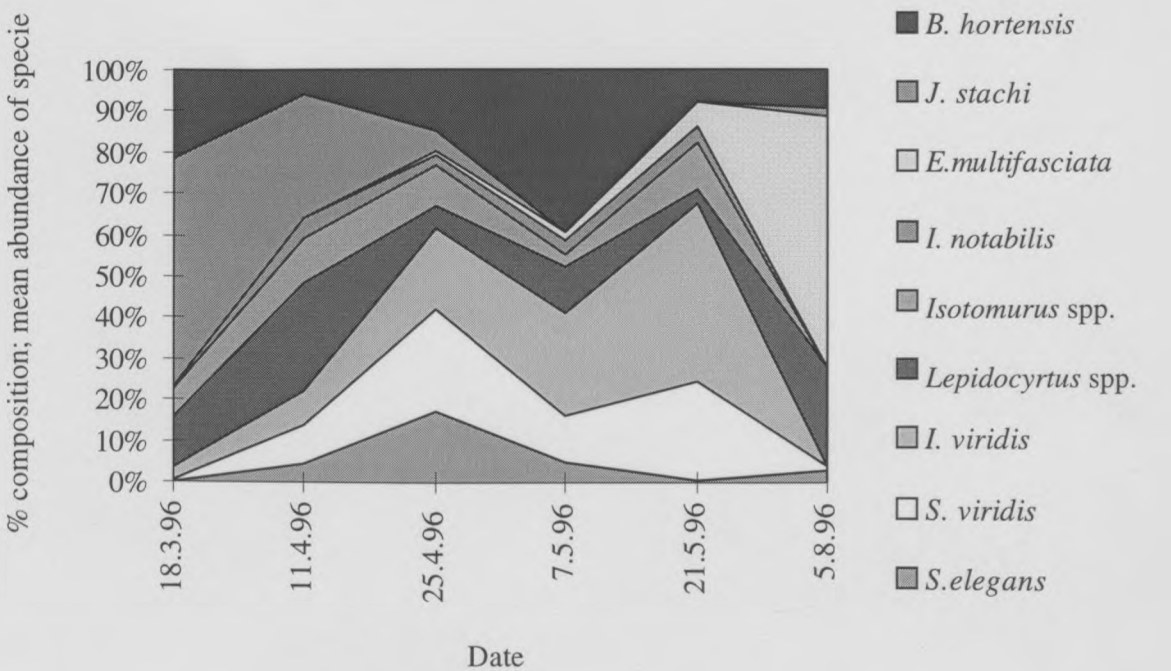


Figure 2.5 Species composition in the middle of barley fields over the growing season.

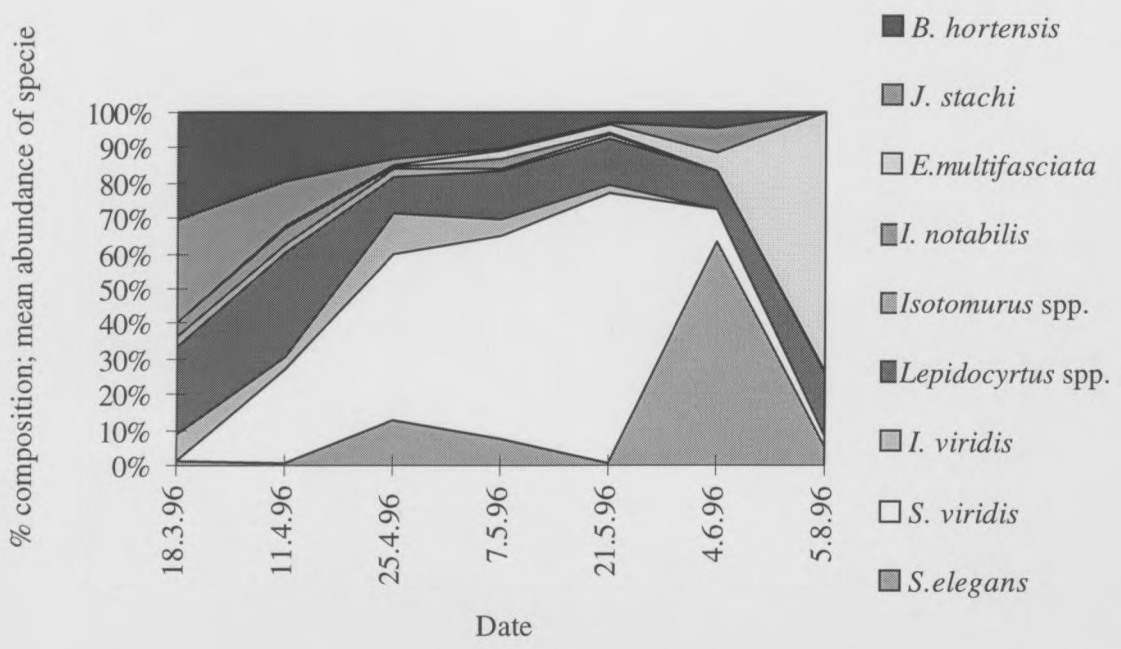
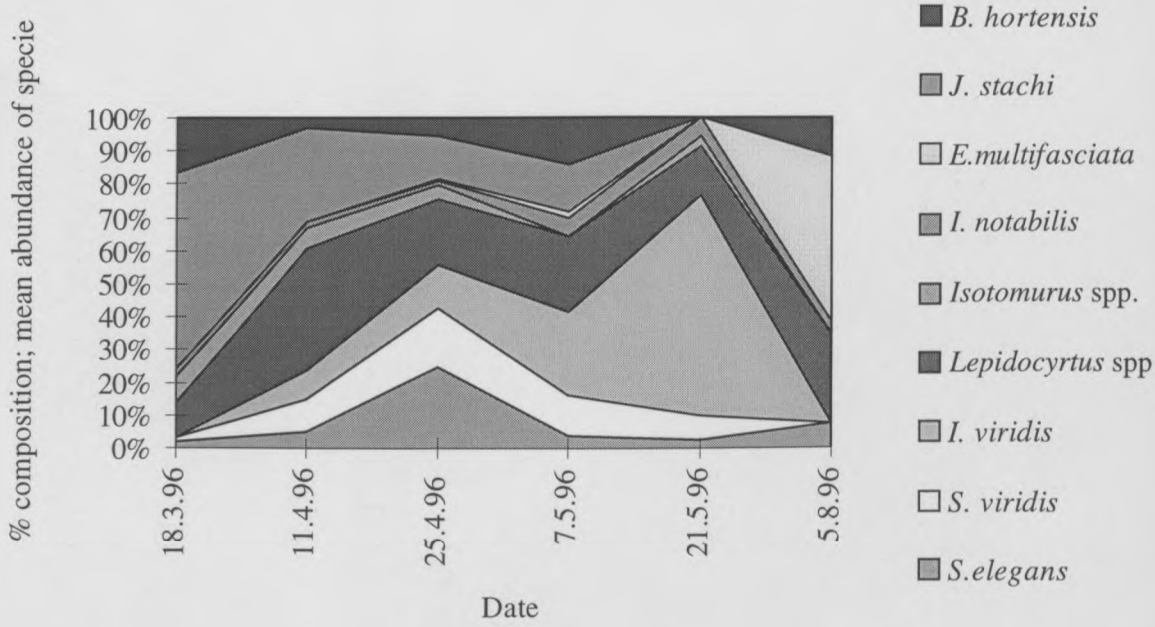


Figure 2.6 Species composition in the middle of pea fields over the growing season.



In the early stages of crop development the community was not dominated by any one species (Figs. 2.3 to 2.6). However, equitability decreased over time. The trends in population changes are shown in Table 2.3. *Sminthurus viridis* was the most abundant species in May in the edges of fields under both crop types although it remained rare in the central sampling positions (Figs. 2.3 to 2.6). However by August the Collembola were dominated numerically by *E. multifasciata* in all fields and sampling positions. The *Lepidocyrtus* species did not noticeably increase in their proportional representation in the fields, but there was at least a two-fold increase in their abundance over time (see Table 2.3).

Table 2.3. Temporal trends in the distribution of Collembola in two spring-sown crops. Values denote initial and final means ± s.d.; results of repeated measures ANOVA

* Only the first four dates were analysed as this species was not trapped on later dates.

Population trends	Species
Increased in abundance as the summer progressed in all fields and both positions:	• *S. viridis* 4.8 ± 6.9, 16.3 ± 32.9, $P < 0.001$; n=7
	• *S. elegans* 2.25 ± 6.7, 92.8 ± 129.8, $P < 0.001$; n=7
	• *E. multifasciata* 0.2 ± 0.6, 88.1 ± 116.2, $P < 0.001$; n=7
Decreased in abundance over spring in all fields and both positions:	• *J. stachi* (*S. violaceus*)17.5 ± 28, 1.5 ± 3, $P = 0.003$; n=4*
	• *B.hortensis* 4.9 ± 11, 2.9 ± 4, $P < 0.001$; n=4*
Decreased in the spring then increased later in the summer	• *Lepidocyrtus* spp. March 14.9± 21.0, May 2.9 ± 3.9, July 31.4 ± 50.2, $P < 0.001$; n=7
Increased in the spring then decreased in the summer	• *I. viridis* March 3.5 ± 6.6, April 12.1 ± 12.8, August 0.5 ± 1.1, $P < 0.001$; n=7
Rare throughout spring; increase in abundance slight and restricted to the field edges	• *Isotomurus* spp. 4.5 ± 6, 1.0 ± 1, $P < 0.001$; n=4*

Certain taxa were trapped only in the early sampling dates. These included *J. stachi* (*S. violaceus*), *B. hortensis*, and *Isotomurus* spp. The latter two taxa were also principally found in the edges of fields. Catches of all species declined in the pea fields after soil disturbance caused by sowing in May - cultivation is known to be detrimental to epigeal populations (Fromm *et al.* 1993b). A concurrent but smaller decrease in the spring barley catches of *S. elegans, I. viridis, Isotomurus* spp. and *B. hortensis* may have been attributable to the application of fungicides, which are harmful to some Collembola (Frampton 1988, 1994), at this time. *S. viridis* and *E. multifasciata* appeared to be unaffected by the chemical applications and both showed late summer peaks in populations.

2.4.3 Species overwintering in the field.

The fields due to be drilled with peas had been left as undisturbed bare soil over winter, and unlike those recently drilled for barley were still undisturbed at the beginning of this study in March. They thereby provided an opportunity to identify those species present in the soil prior to sowing, and hence those most likely to have overwintered there. *J. stachi* (*S. violaceus*), *B. hortensis*, *I. viridis, Isotomurus* spp. and *Lepidocyrtus* spp. were all present as adults in suction samples taken on 18 March.

2.4.4 The effects of position in the field on faunal composition and abundance

There were significantly more species of Collembola found in the edge as opposed to the middle of all the experimental fields (Fig. 2.2; two-way ANOVA for counts averaged over

all dates was $F_{1,22} = 43.13$, $P < 0.001$). Shannon-Wiener equitability indices did show a consistent pattern of species composition and abundance, as previously shown in Fig. 2.2. *Isotomurus* spp., *E. multifasciata* and *I. viridis* tended to be more numerous in the field edges than in the middle (Table 2.4), as did *B. hortensis*. However *S. elegans, S. viridis, Lepidocyrtus* spp, and *J. stachi* (*S. violaceus*) showed no significant differences between the two locations.

Table 2.4. Influence of position and crop type upon the abundance of Collembola. Values denote overall mean ± s.d. Results of repeated measures ANOVA are given.

Consistent effects of position upon abundance over time	Consistent effects of crop type upon abundance over time
• *E. multifasciata* $P < 0.05$ (edge 2.3 ± 12, > middle 0.3 ± 1)	• *E. multifasciata* $P = 0.016$ (barley 2.2 ± 12, > peas 0.6 ± 1)
• *I. viridis* $P < 0.05$ (edge 7.2 ± 10, > middle 3.0 ± 5)	• *I. viridis* $P < 0.001$ (peas 7.3 ± 9, > barley 2.4 ± 3)
• *B. hortensis* $P < 0.001$ (edge 15.9 ± 37, > middle 2.0 ± 4),	• *Lepidocyrtus* spp. $P < 0.05$ (peas 10.5 ± 17, > barley 4.1 ± 6)
• *Isotomurus* spp. $P < 0.001$ (edge 3.1 ± 5, > middle 1.0 ± 2),	• *J. stachi* (*S. violaceus*) $P < 0.05$ (peas 11.9 ± 25, > barley 1.4 ± 2),
	• *S. viridis* $P < 0.05$ (barley 20.8 ± 31, > peas 9.1 ± 19)
	• *S. elegans* $P < 0.05$ (peas 3.9 ± 11, > barley 2.6 ± 5),

2.4.5 The influence of crop type on abundance

In early March, the total collembolan catch in the fields designated to be sown with peas (edge: 143 ± 25; middle 63 ± 12) was much higher than in those in which barley had just been sown (edge 18 ± 2; middle 8 ± 1), probably due to the disturbance caused by sowing.

However by the end of May the situation had been reversed (peas edge 35 ± 26, middle 8 ± 12 ; barley edge 98 ± 17, middle 41 ± 10) as the peas were drilled in early May, and hence the soil surface had been disturbed. For certain species crop type had the major effect upon their abundance (Table 2.4), whilst for others both crop and position were important. Overall, despite significant differences in the catch of species under the different crops there were no clear differences in species presence between peas and barley. This would suggest that species presence alone is not as useful as data including relative abundance.

The differences in temporal population trends between the two crop types could be attributed to several factors: firstly, the different management practices required for two different types of crops, particularly the different sowing dates; secondly, the different canopy types; and thirdly, the different use of pesticides. Different canopy types were encountered between early May when the peas were sown, up until early August (2.8.97 - 6.8.97) when the peas were harvested. Before or after these dates the major difference was between a cereal providing vegetation cover, and bare ground.

2.5 Conclusions

2.5.1 Implications of population dynamics for Collembola as alternative prey items for beneficial arthropods in integrated management systems.

The population dynamics of Collembola in arable fields during spring are of potential interest as springtails are an important prey source for polyphagous predators (for examples, see Bauer 1985, Kennedy 1994, Kielty *et al.* 1996). Overwintering predator populations may be present earlier in the year than pests, and Collembola could be important as an alternative

food source at this time to bolster predator population levels in integrated management systems. This study has shown that many of the species of Collembola that are abundant in the early spring are susceptible to the effects of management for a spring-sown crop.

2.5.2 Implications for sampling schedules

Despite a similar species presence, a consistently different community composition was found in the two spatial sampling positions in this study, and this has important implications for sampling schemes in the future. In particular, this study demonstrated that the position where sampling took place in the field appeared to be a major determinant of community composition. Valid comparisons between treatments and fields can only be made within the parameters defined by a sampling regime specifying the location of sampling. It is equally important to take into account the considerable variation due to temporal effects. It should be emphasised that in monitoring studies of this nature it is vital to use a statistical technique that enables the researcher to differentiate between the effects due solely to time, and the treatment effects that are of greater interest.

This study also showed that differently constructed collembolan communities occurred under different crops and followed different dynamics. Hence for the purposes of monitoring pesticide effects in field situations, it is desirable to take into account the current and the previous crops cultivated.

2.5.3 *Implications for the recovery of populations in the field*

The different community compositions encountered between the edges and middle of fields suggest that the edges may act as sources of recruitment for the arable communities. However, consistent differences in the numbers of species suggest that some species are better adapted to living in the environments encountered in the centres of fields, whilst edge communities are most likely to be determined by the nature of the nearest edge. Alternatively, differences in the abundance of collembolan species could be due to differential predation pressures near the edges of fields (Duffield *et al.* 1996).

The behaviour of populations over winter is important when considering pesticide effects (Vickerman 1992). Species overwintering in the field are more likely to be negatively affected by pesticide applications early in the year before a protective canopy is developed, (unless the overwintering stage is resistant, e.g. eggs were less susceptible to pesticides than juveniles or adults - Chernova *et al.* 1995). The species which were common prior to crop emergence, namely *J. stachi* (*S. violaceus*), *Lepidocyrtus* spp., *Isotomurus* spp., *I. viridis* and *B. hortensis* could experience maximum exposure to pesticide applications as there was no sheltering crop canopy available.

The source of population recruitment could also affect the ability to recover from pesticide applications and soil disturbance. Species that were able to regenerate in the middle of fields could recover faster than those which recolonise from other nearby populations, but would also be at greater risk of initial and residual exposure. Evidence that *E. multifasciata* may have colonised these fields from hedgerows is that: a) no individuals were found overwintering in the field either as adults or eggs; b) a potential source of colonists was

present near hedgerows; and c) the field populations increased over time. Populations of other species may have regenerated *in situ*, particularly those that were present as eggs.

The results presented here demonstrate that a considerable amount of information on Collembola communities can be obtained from a simple and short-term monitoring programme. However it is still desirable to study the population dynamics over a whole season, and under a mature canopy. Ideally this type of experiment should also be repeated over several years so as to provide greater confidence in the variation within the factors involved. Such information is essential to elucidate the mechanisms of exposure to, and recovery from, current pesticide use.

3. The role of hedgerows in the recolonisation of arable fields by epigeal Collembola.

3.1 Summary.

1. The role of hedgerows as reservoirs for beneficial predatory arthropods in agroecosystems has been extensively studied, but their importance as habitats for springtails (Collembola) is largely unknown.

2. In this study the recovery of springtail populations was examined in a spring-sown cereal crop following a physical disturbance due to tillage. To investigate the role of a hedgerow in population recovery, replicated lengths of hedgerow were isolated from the field using exclusion barriers.

3. Areas of the field adjacent to barriered sections of hedgerow developed significantly different population and community structures compared to unbarriered 'controls'.

4. Some species of Collembola were consistently more abundant next to the hedgerow (e.g. *Isotomurus* spp., *Bourletiella hortensis*) than within the field habitat. Certain species (e.g. *Isotoma viridis, Sminthurinus elegans* and *Sminthurus viridis*) appeared to colonise the field from the hedgerow to supplement the field population, whilst for other species (e.g. *Lepidocyrtus* spp.) the major source of recovery was from within the field itself.

5. This study provides the first evidence that hedgerows could be important source habitats for the recovery of collembolan populations in arable fields.

3.2 Introduction

The importance of hedgerows as habitats for the fauna of arable farmland has been extensively studied (e.g. Pollard 1968a, 1968b, Sotherton 1984, 1985, Burel 1996). It is now well recognised that grass banks and hedgerows act as shelters and sources of recolonisation for highly mobile predatory arthropods which can either colonise fields in a wave from the hedgerow by walking, or can be rapidly dispersed by flight over large spatial scales (Dennis 1991, Dennis & Fry 1992). Hedgerows have even been found to be important sources of recolonisation for more poorly dispersive organisms such as earthworms (Hansen *et al.* 1989). The use of field edges as overwintering habitats has been shown for a wide variety of species (e.g. see Dennis 1989a, 1989b, Jensen *et al.* 1989). Field edges (e.g. hedgerows) can act as refugia from which recovery of species populations within arable fields may occur following pesticide applications; species which overwinter in the field are at risk of exposure to winter pesticide applications (Vickerman 1992).

The presence of source populations will be important for recovery following periodic agricultural disturbance including tillage and pesticide applications. These sources of disturbance are known to be detrimental to the species diversity and abundance of Collembola within arable fields (see sections 1.4 and 1.5, and Edwards & Thompson 1973, Heisler 1994b). Pesticides in particular have been found to have long-lasting detrimental effects upon epigeal springtail populations (Filser *et al.* 1995, Frampton 1997b). However the potential of hedgerows as refugia for field-dwelling Collembola has received little attention. Previous work has suggested that hedgerows could be sources of Collembola recovery since species density, diversity and biomass decrease with increasing distance from edges into fields (Chapter 2, Alvarez *et al.* 1997, Reddersen 1997). However the higher abundance and

diversity near field edges is likely to be caused by species which are native to the hedgerow habitat rather than to the arable field itself, and the observed boundary effect may only operate over a minor part of the field depending on its size and shape (Hald & Reddersen 1990). Hence it is still unknown whether hedgerows are important source habitats for the epigeal Collembola characteristically found in arable fields.

This study aimed to determine whether hedgerows act as source habitats of arable field collembolan populations in the spring. Polythene barriers, which effectively block the movement of Collembola (e.g. Gravesen & Toft 1987, Mebes & Filser 1997), were used to isolate sections of hedgerow from the field to test the hypothesis that Collembola recolonise recently disturbed field habitats from hedgerows. The effects of this habitat manipulation upon subsequent population and community development provided information on the recovery strategies of individual species and the importance of hedgerows as refugia for springtails.

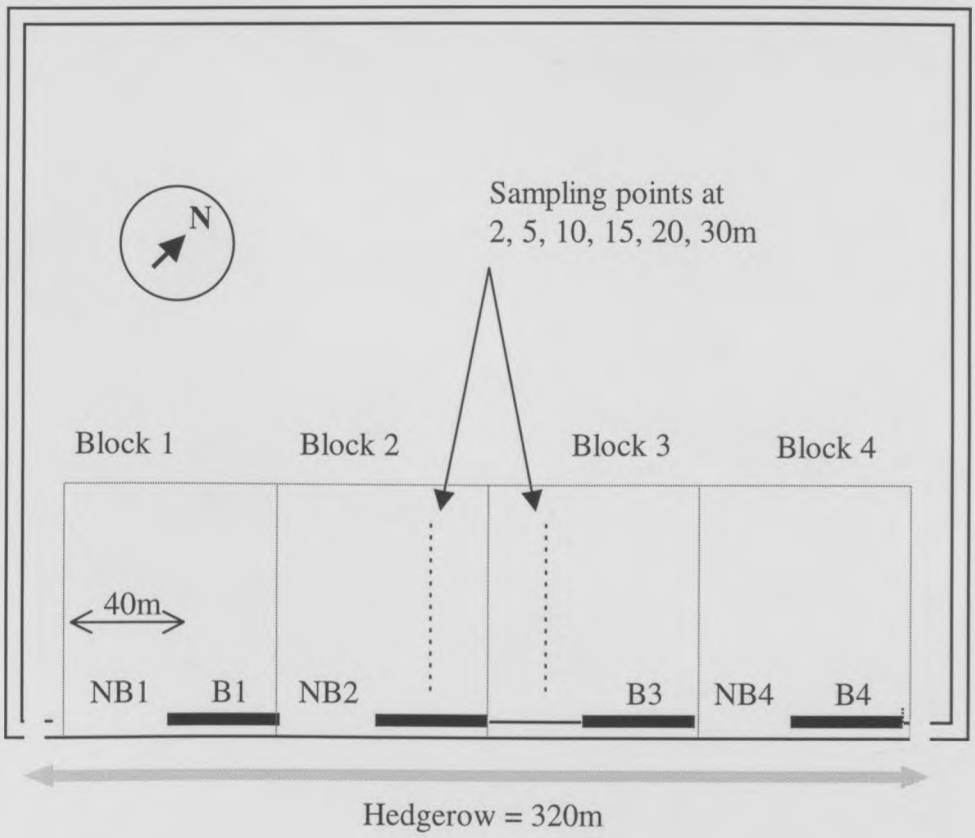
3.3 Materials and Methods:

3.3.1 Study area and experimental design

The study field had been sown with spring barley (cv. Hart) on 16 February 1998. It was located at Longstock on the Leckford Estate in Hampshire, southern England (51° 8' N, 1° 29' W). The soil type was light loam over chalk. No pesticides were applied during the period of this study nor in the previous two years. The most recent pesticide application was Lambda-cyhalothrin, a pyrethroid insecticide applied in November 1995. The field had one continuous edge of mature hedgerow (containing *Sambucus nigra* L., *Crataegus* spp., *Prunus*

spinosa L., and a well-developed mixed herbaceous layer) about 2.5 m tall and aligned from south-west to north-east. Barriers were erected in the field 50 cm from the base of the hedgerow on 18 March. The barriers consisted of polythene sheets 1 m above ground level and dug 25 cm into the soil, hung on rope and supported by wooden posts. 40 m lengths of barriers were interspersed with 40 m lengths of unbarriered hedgerow, and each treatment comparison block was replicated four times (Fig. 3.1).

Figure 3.1 Experimental set-up on a 17.5 ha field of spring barley. The barriers are labelled B1-B4, the unbarriered areas of open hedgerow are NB1- NB4 within the blocks 1-4 (not drawn to scale).



Suction samples were taken using a leaf-blower (Ryobi RSV3100) adapted as described in Stewart & Wright (1995) (see Chapter 2). For each sample, a total area of 0.5 m^2 was sampled, comprising five pooled sub-samples of 10 seconds duration. These were taken randomly within a 1 m^2 area at each of six points along a perpendicular transect from the middle of each barriered or control section. Samples were taken at 2 m, 5 m, 10 m, 15 m, 20 m and 30 m from the hedgerow. Pre-treatment samples were taken before the barriers were erected on 17 March (-1 day), and post-treatment samples were taken on 24 March (+6 days), 5 April (+18 days) and 13 May (+56 days).

3.3.2 Species identification

Samples were stored in 80% methylated spirit. Collembola were removed and examined under a binocular microscope; specimens which were difficult to identify were mounted and examined further using a compound light microscope. Species were identified with the aid of Stach (1947, 1956, 1963), Fjellberg (1980) and Christiansen & Bellinger (1980, 1998). The entomobryid species *Lepidocyrtus violaceus* Lubb. and *L. cyaneus* Tullberg were not differentiated to aid a faster processing of the samples. The Isotomid genus *Isotomurus* spp. were not separated as there is continuing debate on the taxonomy of the constituent species (e.g. see Carapelli *et al.* 1995, 1997; Frati *et al.* 1995).

3.3.3 Statistical analysis

The counts of Collembola from the samples were square root transformed ($\sqrt{(count + 0.5)}$) since in this study this transformation was better than a log transformation in enabling

the data to fulfil the requirements for parametric analysis. The data were tested for normality using the Kolmogrov-Smirnov test (see Sokal & Rohlf 1995) and heterogeneity of variances using Cochran's test (see Underwood 1997). Margalef's species richness, Simpson's dominance index, and the Shannon-Wiener diversity index were produced using the program DIVERSE available in the software package PRIMER (©Plymouth Marine Laboratory 1997; see Carr 1997). These indices were normally distributed and did not require transformation for parametric analysis.

A multifactorial analysis of variance was carried out on the transformed Collembola counts and the untransformed community indices using STATISTICA (© StatSoft Inc. 1984-1995). ANOVAs were carried out using the variables barrier treatment (a fixed factor) and distance from hedgerow (a random factor). The division of the field into blocks consisting of adjacent pairs of control and barrier treatments (Fig. 3.1) was done to overcome potential difficulties in identifying the main effects caused by the variables of interest (i.e. barrier treatment and distance from the hedgerow) due to heterogeneity in environmental conditions within the field. Blocks were included as a random factor in the analysis. In randomised block designs the block interactions with other factors are generally assumed to be absent, which does not affect the testing of the main treatment effects (Sokal and Rohlf 1995). The block effect is not usually tested since variation is expected to occur between blocks due to environmental heterogeneity: hence the use of the blocks. If no heterogeneity had been expected across the field then a two-way ANOVA design could have been used.

Repeated measures ANOVA was carried out using SPSS (© SPSS Inc. 1989-1997) to compare the effects of the factors barrier treatment and distance from hedgerow (both fixed factors) upon repeated measurements of abundance over time. Data were previously tested to ensure compliance with the requirements of repeated measures analysis using the Mauchley test for homogeneity of covariances: where this proved significant the Greenhouse-Geisser

epsilon value was used to adjust the F-tests' degrees of freedom (Kinnear & Gray 1994).

3.4 Results

3.4.1 Effects of the barriers upon species abundance

The most common species encountered were: *Sminthurinus elegans* Fitch, *Sminthurus viridis* L., *Bourletiella hortensis* Fitch, *Isotoma viridis* Bourlet, *Lepidocyrtus* spp., *Isotomurus* spp., *Pseudosinella alba* Schaffer and *Isotoma notabilis* Schaffer. The barriers had no effect upon numbers of *I. notabilis* or *B. hortensis.* Significant differences due to the barrier treatments were found in the counts of *I. viridis, Lepidocyrtus* spp., *Isotomurus* spp., *P. alba,* and *S. elegans* (Table 3.1).

Significantly higher populations were found in the unbarriered areas for *I. viridis* 6 days after the barriers were erected (Fig. 3.2a) and for *S. elegans* 18 days after barrier erection (Fig. 3.2b). A trend for higher abundance in unbarriered areas was found for *S. elegans* 56 days, and for *S. viridis* 18 days, after barriers were erected (Fig. 3.2c), although these patterns were not significant. By the last sampling date the trend for *I. viridis* had been reversed with higher populations present adjacent to the barriers (Fig. 3.2a) although again the difference was not significant. Numbers of *P. alba* and *Lepidocyrtus* spp. were found to vary spatially across the field throughout the experiment, with higher populations present in blocks 1 and 2 (e.g. see Fig. 3.3a). Despite these differences, consistently higher counts were found in the areas adjacent to the barriers for *Lepidocyrtus* spp. (Fig. 3.3b) and *Isotomurus* spp.(Fig. 3.3c). *B. hortensis* was not significantly affected by the presence of barriers but was consistently more common near the hedgerow (Fig. 3.3d).

Table 3.1 Comparisons of the square-root transformed Collembola counts according to barrier treatment and distance from the hedgerow. 'Date' refers to the number of days before or after the barriers were erected.

(NS = no significant difference, P > 0.05; * = P < 0.05; ** = P < 0.01; *** = P < 0.001).

Species	Date	Distance	Barrier	Barrier × distance
I. viridis	- 1	$F_{5,15} = 3.2$*	NS	NS
Isotomurus spp.		$F_{5,15} = 5.0$**	NS	$F_{5,15} = 4.9$**
I. notabilis		NS	NS	NS
P. alba		NS	NS	NS
S. elegans		$F_{5,15} = 5.5$**	NS	NS
S. viridis		NS	NS	NS
B. hortensis		NS	NS	NS
Lepidocyrtus spp.		NS	NS	NS
I. viridis	+ 6	$F_{5,15} = 15.7$*	$F_{1,3} = 4.4$*	NS
Isotomurus spp.		$F_{5,15} = 4.7$**	NS	NS
I. notabilis		NS	NS	NS
P. alba		$F_{5,15} = 4.1$*	NS	NS
S. elegans		$F_{5,15} = 13.1$***	NS	NS
S. viridis		NS	NS	NS
B. hortensis		NS	NS	NS
Lepidocyrtus spp.		NS	$F_{1,3} = 11.9$*	NS
I. viridis	+ 18	NS	NS	NS
Isotomurus spp.		NS	$F_{1,3} = 35.1$*	NS
I. notabilis		$F_{5,15} = 12.4$***	NS	NS
P. alba		NS	$F_{1,3} = 26.6$*	NS
S. elegans		NS	$F_{1,3} = 9.3$*	NS
S. viridis		NS	NS	$F_{5,15} = 3.0$*
B. hortensis		NS	NS	NS
Lepidocyrtus spp.		$F_{5,15}$=5.0**	NS	NS
I. viridis	+ 56	NS	NS	NS
Isotomurus spp.		$F_{5,15} = 4.6$**	NS	NS
I. notabilis		$F_{5,15} = 3.5$*	NS	NS
P. alba		NS	NS	NS
S. elegans		NS	NS	$F_{5,15} = 7.9$***
S. viridis		$F_{5,15} = 5.9$**	NS	NS
B. hortensis		$F_{5,15} = 3.4$*	NS	NS
Lepidocyrtus spp.		$F_{5,15} = 3.2$*	NS	NS

Figure 3.2 The catch of Collembola in a field adjacent to barriered (black circles) and unbarriered (white squares) lengths of a hedgerow on four sampling dates and at different distances into the field. a) Data for *I. viridis*; b) Data for *S. elegans*; c) Data for *S. viridis*. Significant differences due to barrier treatment are denoted by b* = P < 0.05; those due to distance by d* = P < 0.05, d = P < 0.01, b*** = P < 0.001.**

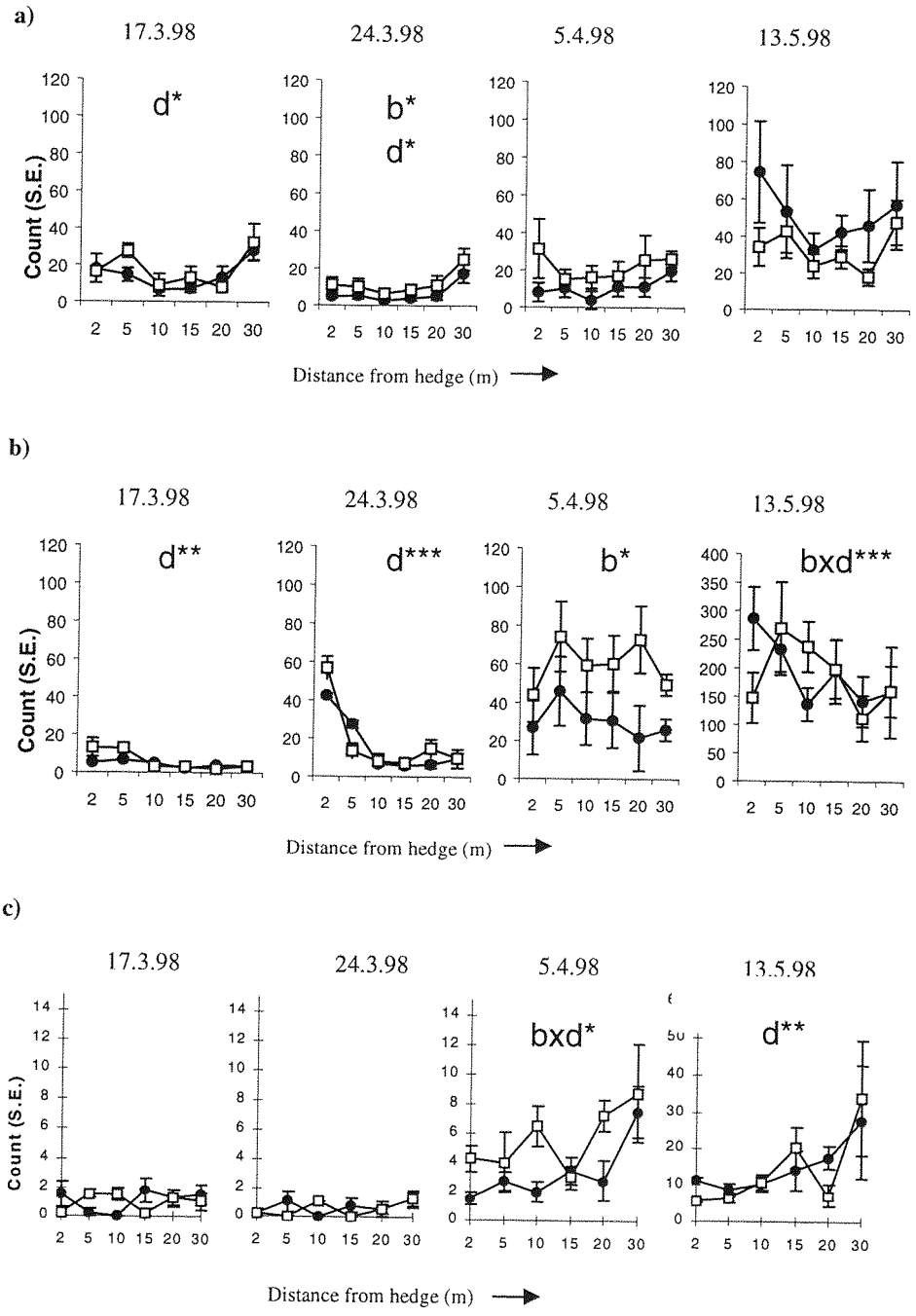
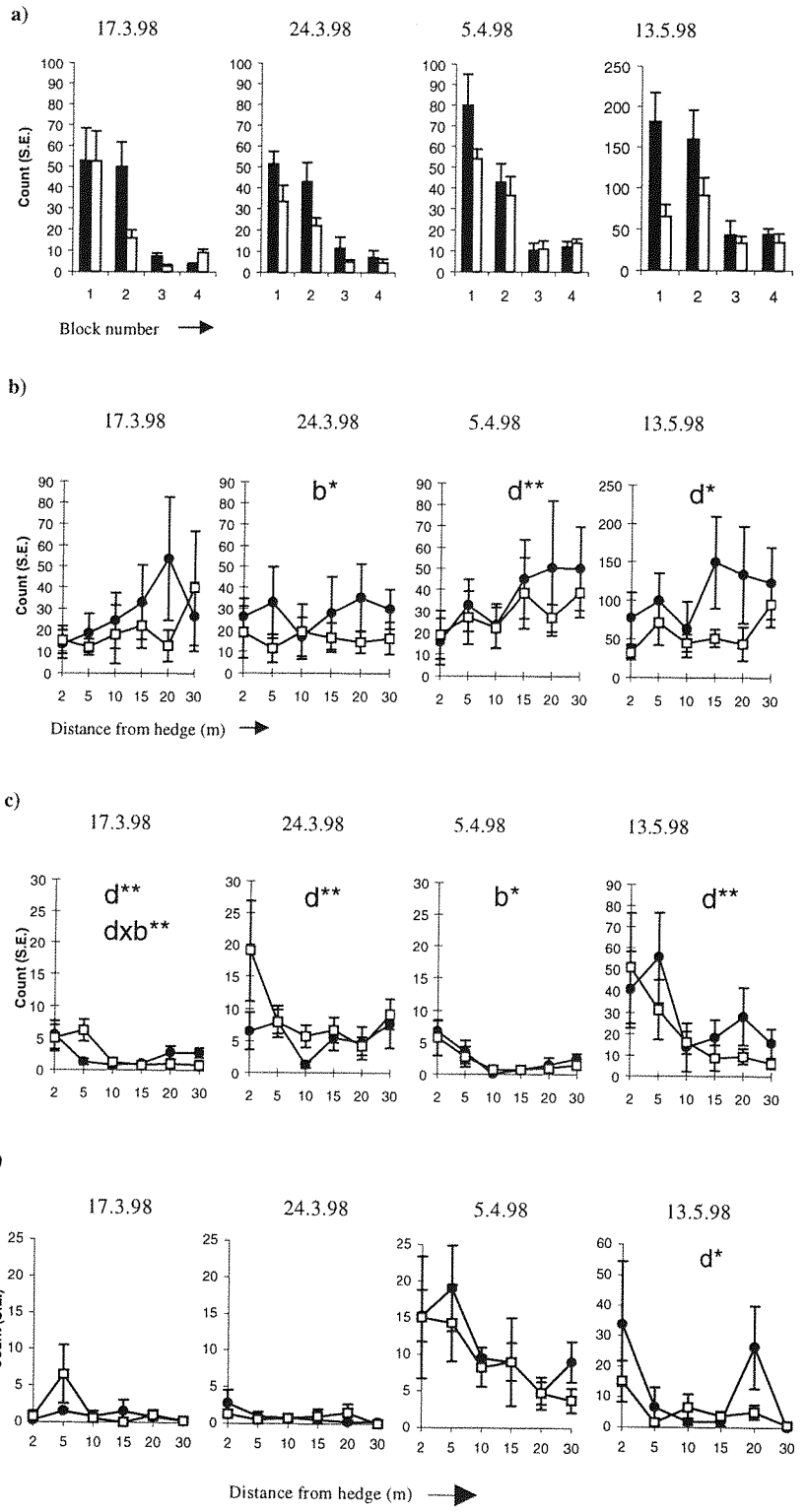


Figure 3.3 Collembola catch in a field adjacent to barriered (black columns or circles) and unbarriered (white columns or squares) lengths of a hedgerow on four sampling dates. a) Spatial distribution among blocks for *Lepidocyrtus* spp.; b) Spatial distribution from the hedgerow for *Lepidocyrtus* spp.; c) Spatial distribution from the hedgerow for *Isotomurus* spp.; d) Spatial distribution from the hedgerow for *B. hortensis*. Significant differences due to barrier treatment are denoted by b* = P < 0.05; those due to distance by d* = P < 0.05, d = P < 0.01.**



3.4.2 Effects of the barriers upon community composition

Field areas adjacent to barriers had a different community composition relative to the unbarriered areas. Significant differences attributable to the erection of barriers were found in the counts for total Collembola and Symphypleona, and in the indices used to estimate species richness and diversity (Table 3.2). These differences occurred mainly three weeks after the barriers were erected, although differences in species diversity and dominance were detected after only one week. A higher diversity was found 5 and 18 days after barrier erection in the unbarriered areas, and this was significant after 18 days (Fig. 3.4a). In contrast a higher dominance was encountered next to the barriers for 6 and 18 days after the barriers were erected, although these differences were not significant (Fig. 3.4b). A significantly higher measure of species richness was encountered in the unbarriered areas 18 days after the barrier erection (Fig. 3.4c). A significantly higher abundance of total Collembola (Fig. 3.5a) and total Symphypleona (Fig. 3.5b) were also detected in the unbarriered areas 18 days after the barriers were put up. However, spatial variation across the field was the major source of variance for arthropleonid species and no significant differences were found according to barrier treatment despite a trend for higher abundance in unbarriered areas in April, which had reversed by May (Fig. 3.6a).

Table 3.2 Comparisons of square-root transformed total collembolan counts and species diversity indices according to barrier treatment and distance from the hedgerow. 'Date' refers to the number of days before or after the barriers were erected.

(NS = no significant difference, P > 0.05; * = P < 0.05; ** = P < 0.01; *** = P < 0.001)

Species	Date	Distance	Barrier	Distance × barrier
Total Collembola	- 1	$F_{5,15} = 3.1$*	NS	NS
Symphypleona		$F_{5,15} = 13.0$***	NS	NS
Arthropleona		NS	NS	NS
Richness		NS	NS	NS
Shannon-Wiener		NS	NS	NS
Simpson		NS	NS	NS
Total Collembola	+ 6	$F_{5,15} = 6.7$**	NS	NS
Symphypleona		$F_{5,15} = 9.6$***	NS	NS
Arthropleona		NS	NS	NS
Richness		NS	NS	$F_{5,15} = 3.9$*
Shannon-Wiener		NS	NS	NS
Simpson		NS	NS	NS
Total Collembola	+ 18	NS	$F_{1,3} = 14.8$*	NS
Symphypleona		NS	$F_{1,3} = 20.0$*	NS
Arthropleona		$F_{5,15} = 3.8$*	NS	NS
Richness		NS	$F_{1,3} = 10.9$*	NS
Shannon-Wiener		NS	$F_{1,3} = 25.3$*	NS
Simpson		NS	NS	NS
Total Collembola	+ 56	$F_{5,15} = 4.5$*	$F_{1,3} = 11.2$*	NS
Symphypleona		$F_{5,15} = 7.2$**	NS	$F_{5,15}$=4.7**
Arthropleona		NS	NS	NS
Richness		$F_{5,15} = 8.8$***	NS	NS
Shannon-Wiener		NS	NS	NS
Simpson		NS	NS	NS

Figure 3.4 Differences between community composition in areas adjacent to barriered (B) and unbarriered (NB) lengths of a hedgerow on four sampling dates and at different distances into the field. a) Shannon-Wiener diversity; b) Simpson's index of dominance; c) Margalef species richness. Significant differences due to barrier treatment are denoted by b* = P < 0.05; those due to distance by d* = P < 0.05, d = P < 0.01, d*** = P < 0.001.**

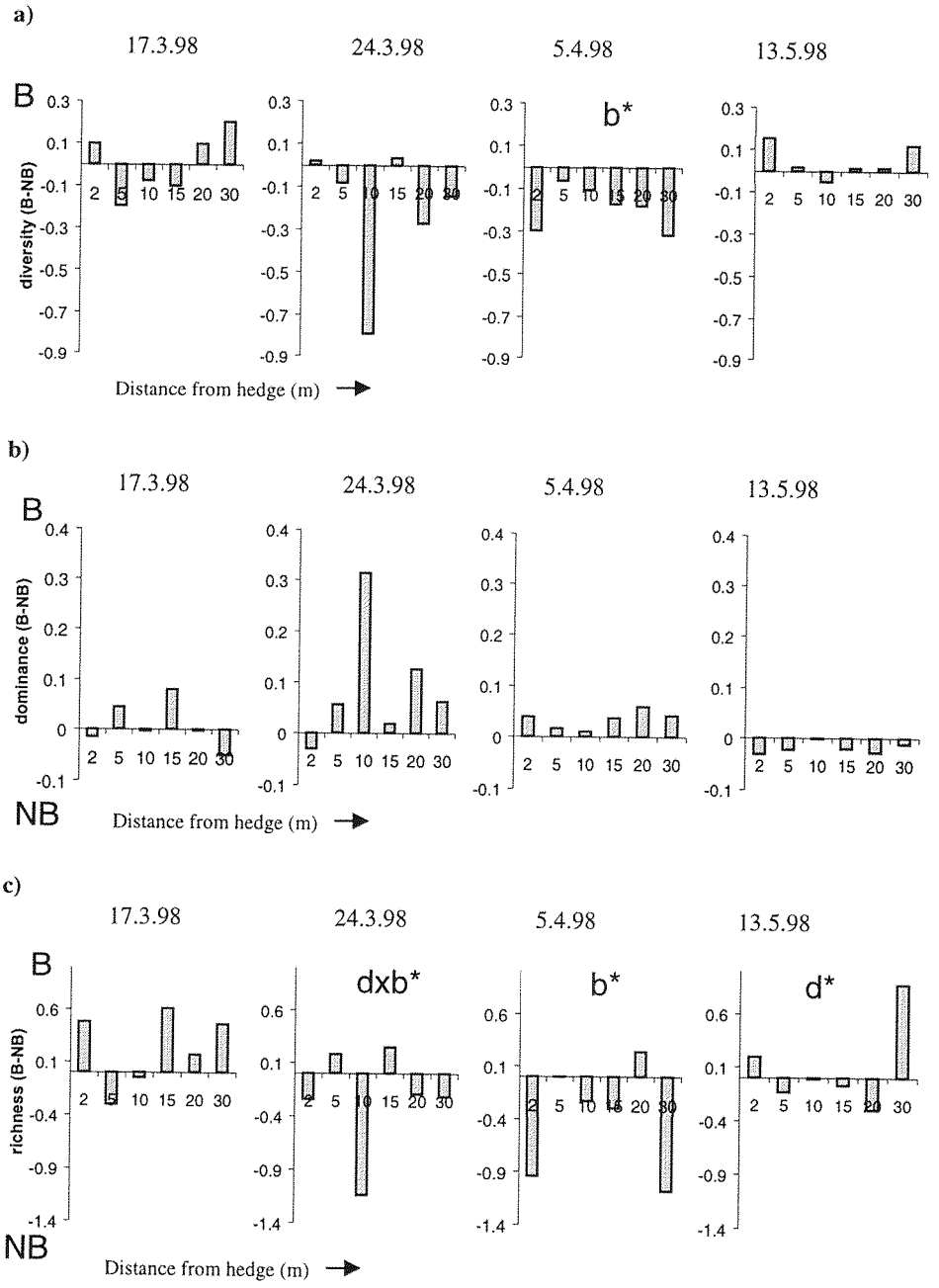


Figure 3.5 The catch of Collembola in a field adjacent to barriered (black circles) and unbarriered (white squares) lengths of a hedgerow on four sampling dates and at different distances into the field. a) total collembolan abundance; b) total Symphypleona. Significant differences due to barrier treatment are denoted by b* = P < 0.05; those due to distance by d* = P < 0.05, d = P < 0.01, d*** = P < 0.001.**

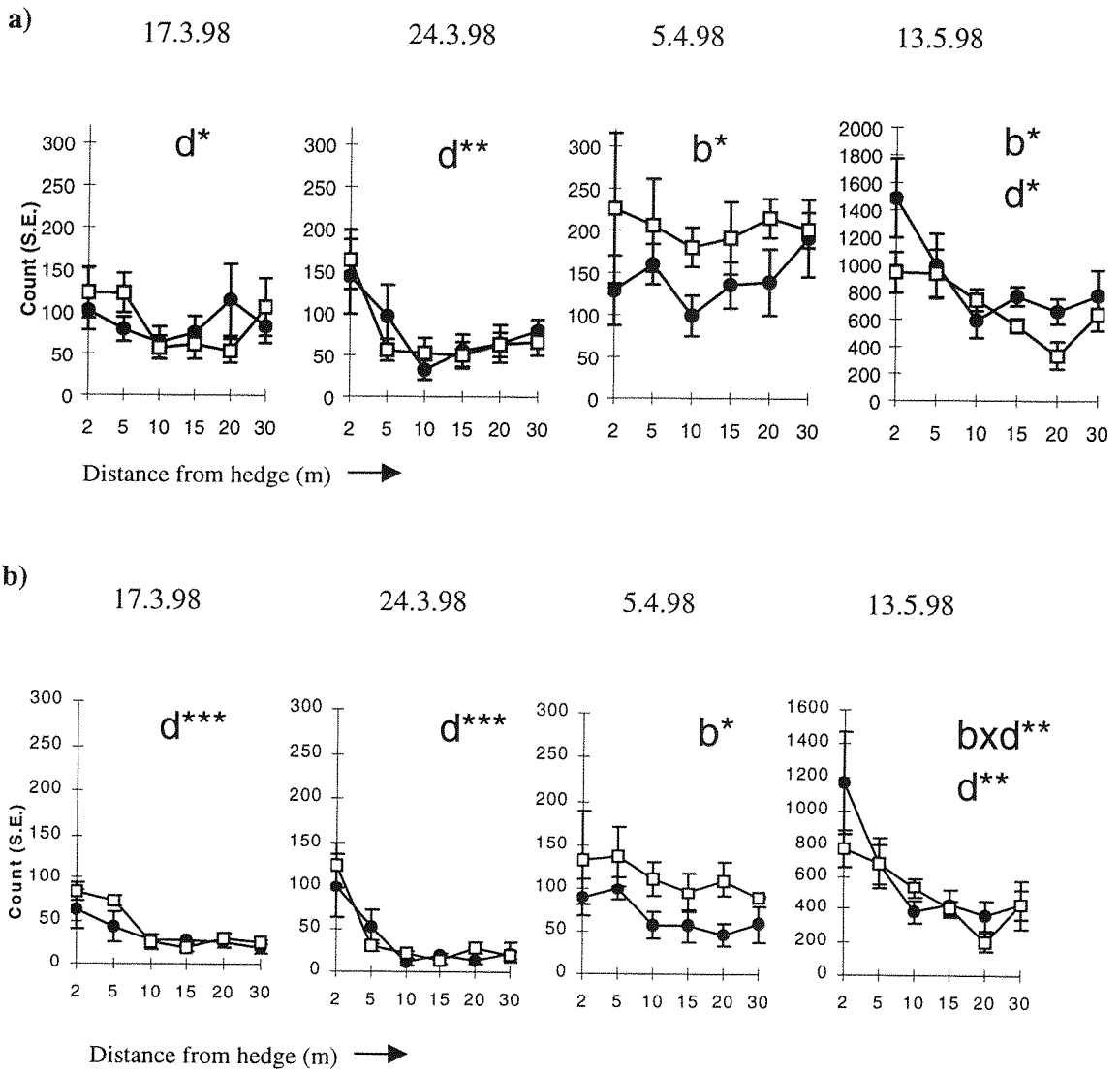
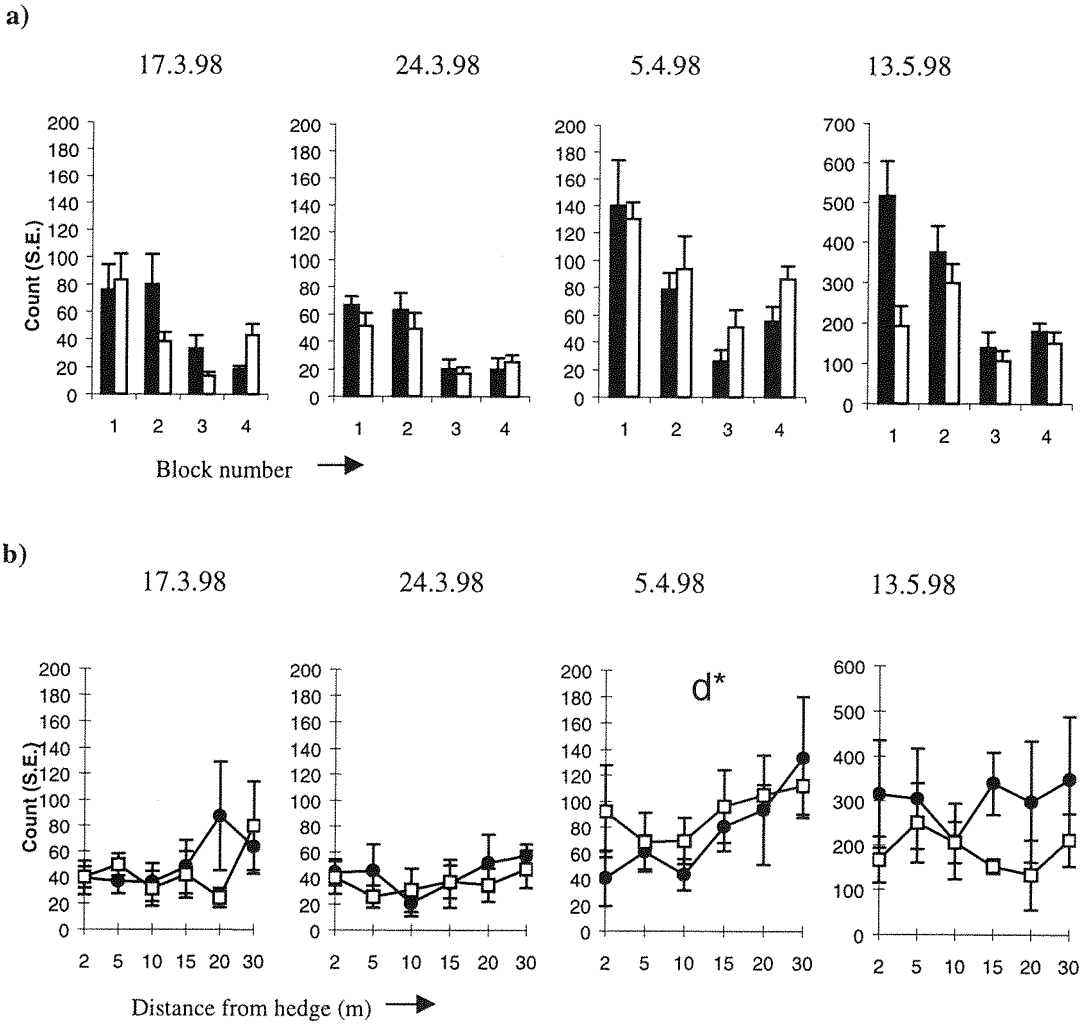


Figure 3.6 Abundance of Arthropleona in a field adjacent to barriered (black columns or circles) and unbarriered (white columns or squares) lengths of a hedgerow on four sampling dates and at different distances into the field. Spatial distribution of total Arthropleona a) between blocks; and b) with distance from the hedgerow. Significant differences due to barrier treatment are denoted by b* = P < 0.05; those due to distance by d* = P < 0.05, d = P < 0.01, d*** = P < 0.001.**



3.4.3 Distance from the hedgerow

Isotomurus spp. remained more common near the hedgerow throughout the study (Fig. 3.3c), as did *B. hortensis* (Fig. 3.3d). The counts of *I. viridis, Isotomurus* spp. and *S. elegans* differed significantly with distance from the hedgerow before (-1 day) and one week (+6 days) after the barriers were erected. *I. viridis* was more numerous within the field whilst the other two species were more common near the hedgerow. *S. viridis* was consistently more common within the field than the edge (Fig. 3.2c), as were the *Lepidocyrtus* spp. (Fig. 3.3b). By the last sampling date most species' spatial distributions showed significant differences due to distance from the hedgerow (Table 3.1).

Generally the Arthropleona tended to become more numerous with distance into the field although this was only significant in April (Table 3.2; Fig. 3.6b). The opposite was true for Symphypleona, which tended to dominate the collembolan community in the edge of the field (Fig. 3.5b). A significant effect of distance from the hedgerow on symphypleonid abundance was encountered on all the sampling dates except early April. Species richness and diversity tended to decrease with distance into the field, although this difference was only significant for species richness on the last sampling day in May (Table 3.2).

3.4.4 Differences over time

For all species, there was a significant change in abundance through time (repeated measures ANOVA, $P < 0.01$). Significant interactions with time were also detected for barrier treatment and distance, suggesting that the treatments had different effects over time (a lack of interaction of time with treatment would imply that the treatment areas differed both before

and after the different treatments were applied - Green 1993). Significant time by barrier interactions were found for *I. viridis* ($F_{2,85} = 6.4$, $P < 0.01$), *S. elegans* ($F_{2,66} = 3.6$, $P < 0.05$), *Lepidocyrtus* spp. ($F_{2,82} = 3.2$, $P < 0.05$), *P. alba* ($F_{2,51} = 4.0$, $P < 0.05$), and *I. notabilis* ($F_{2,56} = 4.1$, $P < 0.05$). These results support those from the analysis for each date, suggesting that significant differences in time trends were found according to the erection of barriers, hence the barriers caused changes in abundance within each area. No significant interactions with the barrier treatments were found for *Isotomurus* spp., *S. viridis* or *B. hortensis.* However the two latter species were found to have a significant time by distance interaction (*S. viridis* $F_{8,64} = 3.1$, $P < 0.01$, *B. hortensis* $F_{9,65} = 2.1$, $P < 0.05$), suggesting differences in abundance trends over time with distance from the hedgerow.

Total counts for Collembola, Arthropleona and Symphypleona, and the Margaleff species richness, Shannon-Wiener diversity and Simpson's dominance indices also showed significant differences between dates ($P < 0.001$) reflecting concurrent changes in abundance and species numbers over time. Significant interactions were also found between changes in abundance over the successive sampling dates and the barrier treatments for total Collembola ($F_{2,67} = 6.2$, $P < 0.01$), Symphypleona ($F_{2,56} = 3.6$, $P < 0.05$), Arthropleona ($F_{2,69} = 5.1$, $P < 0.01$), and species richness ($F_{3,105} = 3.8$, $P < 0.05$), diversity ($F_{3,108} = 3.9$, $P < 0.05$) and dominance ($F_{2,78} = 4.7$, $P < 0.05$). These again suggest that time trends for these measures of community structure differed significantly between the treatment levels.

3.5 Discussion

The species trapped in this experiment consisted largely of those known to be common in agroecosystems in springtime in Britain (e.g. Frampton 1989, 1994, Frampton *et al.* 1992). Consistent with previous findings reported in Chapter 2 and Alvarez *et al.* (1997), *B. hortensis* and *Isotomurus* spp. were found to be common only near the hedgerow whilst *S. elegans* and *S. viridis* were found throughout the sampling area in the field. However, the previous study found that *I. viridis* was only common in the edges of fields, whilst in this study substantial populations were found within the field itself.

The barrier treatment was designed to differentiate between recovery sources within the field itself and dispersal sources from the hedgerow. Since Collembola tend to be regarded as poor dispersers, differences were unlikely to be detected only 6 days after the barriers were put into place; on the other hand, the final sampling occasion happened 56 days after the barriers were set up and by then differences due to the barriers were less likely to be detected due to dispersal across the adjacent barriered and unbarriered areas. Differences due to barriers were mainly detected 18 days after their erection. Sampling was originally planned to occur at weekly intervals; however wet weather conditions precluded sampling from taking place as frequently as would have been desirable.

The abundance of *I. viridis, S. elegans, S. viridis* and total Symphypleona was significantly higher in the unbarriered than in the barriered areas. The effect was transient, with significant differences usually found in early April, but by mid May populations had become more homogeneously distributed throughout the sampled area. The higher abundance in the unbarriered areas suggested that these groups mainly moved from the hedge into the

field, and the barriers blocked this colonisation. Not all species were similarly affected and this may be due to variations in the methods of dispersal used by different species.

The opposite pattern was found for *Isotomurus* spp. and *Lepidocyrtus* spp. In these taxa a significantly higher abundance was recorded in the barriered areas as compared to the controls. This difference between the barrier treatments may be due to the prevention of movement by predators or competitors from the hedgerow into the field. Barriers are known to prevent colonisation by predatory arthropods (Gravesen & Toft 1987, Kennedy 1988). If predation and competition pressures were reduced (by exclusion of predators and other Collembola species), then some Collembola populations could increase to a higher abundance in the barriered areas, than in the areas adjoining open lengths of hedgerow.

No differences in abundance of *B. hortensis* or *I. notabilis* between barriered and unbarriered plots were detected. This suggests that these species may be more mobile, or that predation and competition pressures were not strong (these species were never found in great abundance whether in barriered or unbarriered areas), or that the barriers may simply not have provided an obstacle. The use of the barriers to prevent movement could be limited as individuals could have climbed the barrier itself or dropped or been blown from the vegetation above the barrier level. The climbing of trees for potential dispersal has been described for several species (e.g. see Bowden *et al.* 1976, Farrow & Greenslade 1992). Further studies are required in order to identify the movement strategies used by different species for recolonisation. The isolation of hedgerow sections could be improved by erecting higher barriers or completely covering the hedgerow vegetation.

A variety of species diversity indices were used to investigate the community composition in the field adjacent to barriered and unbarriered areas. The relative merits of such indices have been discussed by Magurran (1988) and by Cousins (1991); the major limitation of such indices is that they are unreliable for comparing diversity between different

habitat types. This was not a problem in the current study, which involved one crop. Differences in species richness, diversity, and dominance were produced by the barrier treatments. A higher diversity and species richness was found in the unbarriered areas, whilst a higher dominance was found in the areas adjacent to the barriers. These changes occurred quickly as differences were detected within two weeks of the barrier erection. The influence upon the field community was transient as few significant differences were found by the last sampling date in May.

Some species appeared to have recovery sources within the field itself. This within-field recovery of Collembola has been previously reported and attributed to predator exclusion by Duffield & Aebischer (1994). In the current work, *I. viridis*, *Lepidocyrtus* spp., *S. elegans* and *S. viridis* were all present 30 m into the field even at the start of the experiment; this presence may have resulted from earlier colonisation prior to barrier erection (tillage disturbance had occurred a month before sampling began), or from populations permanently located within the field. The higher population levels of *I. viridis, S. viridis* and *S. elegans* in the unbarriered areas however suggest that movement from the hedgerow was interrupted by the erection of barriers. Both *S. viridis* (Maclagan 1932a, Wallace 1968) and *S. elegans* (Chapter 4, Alvarez *et al.* 1997) are known to survive as eggs during certain disturbance events. These two species might survive disturbance by tillage as diapausing eggs although this hypothesis requires further investigation. *Lepidocyrtus* spp. were the only group to have had consistently higher populations in the barriered areas, suggesting that recovery sources were present within the field and that the hedgerow was not an important source of field populations. Neither *L. cyaneus* nor *L. violaceus* are known to aestivate, and they are frequently captured in samples taken in winter (Chapters 2, 4; Joosse 1969 also found winter-active *L. cyaneus* in a forest ecosystem), suggesting that they overwinter as adults in the field.

3.6 Conclusions

The different community compositions found along the transects from the edge into the field suggest that the hedgerow acted as a source of recruitment for the open field community. Some species colonised the recently tilled field from populations in the hedgerow, and some species were only present next to hedgerows and may not be truly field-dwelling Collembola (e.g. *B. hortensis*). The extent to which early spring colonisation determines the successive population structure in the field would however require a longer term investigation. Further work is also needed to elucidate the mechanisms determining population levels in the field beyond the barriered areas, in particular how predation and competition are involved in determining the collembolan community composition. This study has shown that hedgerows are important sources of population recovery for some of the Collembola of arable fields.

4. The effects of drought upon epigeal Collembola from arable soils.

4.1 Summary

1. Springtails (Hexapoda, Collembola) are usually associated with moist microhabitats. However, some species show adaptations to ecosystems subjected to periodic desiccation. This study examined the effects of short-term drought conditions upon epigeal Collembola collected from arable fields.

2. An emergence trap was used in the laboratory to investigate collembolan activity, particularly the emergence of newly hatched juveniles from soils subjected to a simulated drought and to varied levels of simulated rainfall.

3. The hatching of *S. elegans* and *S. viridis* from overwintering soils suggests these two species can overwinter as eggs within fields.

4. Addition of water to soils subjected to a four month simulated drought resulted in synchronised emergence of juveniles of *Sminthurinus elegans*, *Sminthurus viridis* and *Bourletiella hortensis*. Since anhydrobiotic juveniles were not found in the soil these juveniles are likely to have recently hatched from eggs in the soil.

5. The same species emerged when desiccated soil samples were treated with simulated heavy rainfall. No emergence occurred in soils which received no water, whilst only a few juveniles were present under a regime of the lowest monthly rainfall recorded for the area in spring.

6. This study provides evidence that in northern European arable systems some epigeal Collembola can survive considerable periods of drought as eggs, whose emergence is triggered by rainfall. These findings have implications for the effects of predicted climatic changes upon collembolan populations, the recovery of collembolan communities

following disturbances (e.g. pesticide applications, tillage) in agroecosystems, and also provide a plausible mechanism for dispersal of Collembola as wind-blown eggs.

4.2 Introduction

The incidence of droughts has increased over recent years in temperate areas such as the UK, where the climate has been predicted, and appears, to be getting warmer and drier (e.g. Markham 1996). These changes in climate, generally attributed to global warming, are predicted to produce changes in the British flora and fauna and are therefore the subject of numerous studies (e.g. Cummins *et al.* 1995, Masters *et al.* 1998b, 1999). Effects are most likely to influence organisms which are known to be sensitive to humidity changes. Collembola are likely to be influenced by the occurrence of drought, since they are prone to desiccation as most species lack true tracheal systems and breathe through their integument. Humidity and temperature are known to be critical factors in their distribution, as has been previously discussed in the introductory chapter (Joosse & Groen 1970, Verhoef 1981, Verhoef & van Selm 1983). Experiments carried out by Hodkinson *et al.* (1998) on the effects of global climatic change in northern Sweden suggested that moisture was a greater limiting factor than increased temperature in determining changes in collembolan population abundance and community composition.

Certain species of Collembola have become adapted to periodically dry environments. Work carried out in Australian deserts and in dry Mediterranean ecosystems has shown that some Collembola have several strategies for coping with dry conditions (Greenslade 1973, 1982). These are: morphological and physiological adaptations to tolerate high temperatures and low humidities; inactive, desiccated drought-resistant adult or juvenile stages which can

be reactivated by moisture, known as anhydrobiosis and ecomorphosis; and desiccation-resistant eggs, which can hatch when humidity increases (e.g. Greenslade 1981). A desiccation-resistant coating to eggs can be provided by faecal pellets (Poinsot 1970, 1971). These adaptations have been found in members of both symphypleonid and arthropleonid Collembola. Eggs may represent a resistant stage in collembolan life histories (Leinaas & Bleken 1983). The avoidance of summer drought by aestivation has been detected in *Sminthurus viridis* L. (Maclagan 1932a, Wallace 1968), *Onychiurus meridiatus* (Argyropoulou & Stamou 1993), *Anurida maritima* (Joosse 1966), *Tetracanthella sylvatica* (Takeda 1976) and *Lepidocyrtus lignorum* (Leinaas & Bleken 1983). The latter authors suggested that a state of slow development (quiescence) was occurring in overwintering populations, rather than a diapause. *Folsomides angularis* and *Brachystomella parvula* were reported to survive through dry Mediterranean summers in an anhydrobiotic state (Poinsot 1968, 1974).

The potential effects of drought on the majority of the collembolan species of temperate agroecosystems remains unknown. In arable fields, Collembola are widespread and play an important role in decomposition and in maintaining soil structure (Naeem *et al.* 1995, Vreeken-Buijs & Brussaard 1996). They are also an alternative food source for beneficial predators of importance for integrated pest management (IPM) (e.g. Kennedy 1994). Long-term studies have suggested that the use of some pesticides produce strong detrimental effects upon collembolan populations (Vickerman 1992, Filser 1995b, Frampton 1997a, 1997b). Aestivation and diapause as eggs, or as anhydrobiotic adults or juveniles, has implications both for the exposure and recovery of Collembola subject to pesticide use in arable fields (section 1.6). It could lead to reduced exposure to pesticides and changes in the overall susceptibility of field populations if eggs and adults have different susceptibilities to pesticides (Chernova *et al.* 1995).

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

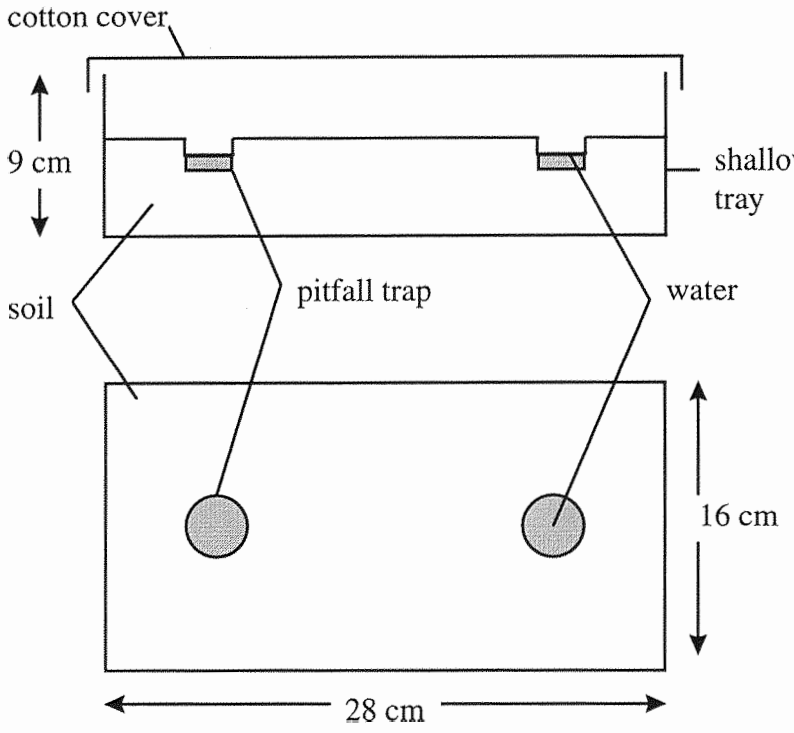
4.3 Materials and methods

4.3.1 Design of the emergence traps.

Emergence traps were designed to be used in the laboratory to trap live, surface-active arthropods from field-collected soils. The traps comprised plastic trays (each 28 × 16 × 9 cm) half-filled with arable field soil (900g), which were kept in the laboratory at room temperature (20-25° C). Two pitfall traps (Petri dishes 3.5 cm in diameter, 1 cm deep) were placed in the trays such that their rims were level with the soil surface, and filled with water (Fig. 4.1). A drop of liquid detergent was added to the water in the traps to reduce its surface tension. Trays were covered with cotton cloth of mesh size 200-250 micrometers and kept in a room with closed windows to prevent colonization from external sources. The contents of the pitfall traps were collected weekly, and were examined under a binocular microscope for

the organisms present. The use of pitfall traps was preferred to soil sampling as it ensured that the organisms captured were alive and active during the experiment and thereby could give a measure of the hatching of individuals.

Figure 4.1 The traps used to detect emergence of surface-active Collembola from field collected soils. Scale 1:3



The efficiency of the pitfall traps was tested by releasing a known number of wild-caught Collembola into each of four replicate emergence traps containing defaunated soil (heated to 150° C). The species released were: *Sminthurus viridis, Sminthurinus elegans* Fitch, *Isotoma viridis* Bourlet, *Deuterosminthurus* spp., and *Lepidocyrtus* spp. Since Collembola can reproduce in the soil trays, the percentage recapture rate was calculated using the total catch after one week in order to ensure that the catch only included the original Collembola released.

4.3.2 Egg survival in the laboratory.

To investigate the presence of Collembola in fields in the early spring prior to crop sowing, ten trays of surface soil (the top 20 cm) were taken from six randomly chosen locations in the centres of two fields ('Scrapps' and 'Danny') in the Manydown Company Estate, Wooton St Lawrence, Hampshire (51° 16' N, 1° 10' W). The two fields were chosen as they had similar cropping and pesticide application histories although slightly different soil types (calcareous silty clay loam and flinty clay loam respectively). Samples were collected on 16 March 1996, before the crop had been drilled and hence reflected a potential overwintering habitat. Both soil types were treated identically. Soil was passed through a 3.5 x 20 mm rectangular coarse sieve to ensure a uniform mixing of the top soil layer, and divided into trays as described above. The trays were randomly allocated to positions on a work bench, and were incubated under controlled laboratory conditions (20-25° C; light: dark 12:12) for two months. The soil was kept moist by watering with a hand-held mister every two days or as required to maintain high humidity levels. Contents of the pitfall traps were recorded weekly for eight weeks. The soils were then allowed to dry out during four months in the laboratory to represent a worst-case scenario by simulating a long summer drought. The dryness of the soil was verified by calculating its moisture content in a sample taken from each tray: heating for 24 hours at 105° C revealed a water content which was less than 5% (water content levels of 20% are considered as relatively dry in field experiments - e.g. Amellal *et al.* 1998). The traps were reset for one week and found to contain no Collembola, after which soils were watered again to simulate rainfall. The Collembola catch was then recorded at weekly intervals for four weeks.

4.3.3 Effects of different simulated rainfall treatments.

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

The trays were then randomly allotted to a treatment. Three simulated rainfall treatments were used: no water (control simulated drought); 1.9 mm per week (minimum realistic rainfall); and 23.7 mm per week (maximum realistic rainfall). These figures were calculated from the 1961-1996 data on rainfall in Hampshire from March-May (UK Meteorological Office data, as above). Water was applied for between 1-4 minutes in each tray every three days, using a hand-held mister and sprayed uniformly over the soil surface. To prevent the complete flooding of the trays excess water was allowed to drain out through a small hole in the base of the plastic container. These treatments were continued for six weeks, during which pitfall contents were examined twice a week. In order to verify that the differences in catches of emerging Collembola were due only to the different water treatments, after this time all the trays were watered with the average rainfall equivalents (12.5 mm per week) and the catches were recorded twice a week for a further two weeks.

4.3.4 Taxonomic identification.

Species were identified using a binocular microscope; difficult specimens were mounted and examined using a compound light microscope. Identification was carried out with the aid of Christiansen & Bellinger (1980, 1998), Fjellberg (1980) and Stach (1947, 1956, 1963). *Lepidocyrtus cyaneus* and *L. violaceus* were not distinguished because of taxonomic problems, and are referred to in the text as *Lepidocyrtus* spp.

A particular problem that was encountered with the identification of these species was the differentiation between *Isotoma viridis* and *I. anglicana.* Christiansen & Bellinger (1980, 1998) described *I. viridis* as having the manubrial thickening unidentate, equivalent to Fjellberg's (1980) 'simple', whilst *I. anglicana* has a bidentate manubrial thickening (Fjellberg's 'free teeth'). In addition, Fjellberg differentiated these two species on another character: *I. anglicana* has the median pair of labral papillae only slightly smaller than the lateral whilst in *I. viridis* the median pair of labral papillae are much smaller than the lateral. However these characters are variable (Fjellberg 1980, Christiansen & Bellinger 1998), and discussion has continued as to the taxonomic validity of these species. Hence in this study I have referred to these species consistently, and conservatively, as *I. viridis.*

4.3.5 Statistical analysis

The pitfall catch was $\log_{10}$ transformed and tested to verify that it fulfilled the assumptions required for parametric analysis, i.e. (1) for the assumption of normality I used the Kolmogorov-Smirnov statistic to test for a significant difference from normal distribution; (2) to test for homogeneity of variance I used Bartlett's tests and F_{max} tests; (3) and in particular for using a repeated measures model for analysis of variance I tested the hypothesis

of sphericity of the variance-covariance matrix (Kinnear & Gray 1994). I used Mauchley's test for sphericity and where this was significant the degrees of freedom for the F-ratio were adjusted using the Greenhouse-Geisser value for epsilon calculated in SPSS ((© SPSS Inc. 1989-1997)(Kinnear & Gray 1994).

Repeated measures ANOVA was carried out in order to compare the catches of Symphypleona or Arthropleona over time among simulated rainfall treatments (a fixed factor) and between soils (a fixed factor). For the rainfall simulation experiment the catch from the first 6 weeks (when the soil trays received different treatments) was analysed separately from data for the final 2 weeks (when all soils received the same rainfall simulation treatment).

4.4 Results

4.4.1 Efficiency of the emergence traps

The recapture rates of five species of Collembola in the emergence traps are shown in Table 4.1. The recapture rate varied between 42.1% (SE 20.5) for *Deuterosminthurus* spp. to 90.1% (SE 3.5) for *Sminthurinus elegans*, hence these traps were successful in trapping diverse species of mobile epigeal Collembola in a controlled laboratory situation. The low capture rate for some species was caused by high mortality of the individuals released (which were found dead on the soil surface).

Table 4.1. Recapture rates one week after Collembola were released into the emergence traps in order to test their efficiency.

Species	Mean % recapture (SE; sample size)
Lepidocyrtus spp.	54.6 (12.2%; n = 62)
Sminthurus viridis	57.2 (12.7%; n = 35)
Isotoma viridis	62.7 (13.6%; n = 130)
Sminthurinus elegans	90.9 (3.5%; n = 117)
Deuterosminthurus spp.	42.1 (20.5%; n = 74)

4.4.2 Survival of eggs following a four-month simulated drought

Captures previous to the period of simulated drought showed that Arthropleona, comprising *I. viridis, Isotomurus* spp., and *Lepidocyrtus* spp., were present as adults in the 1996 spring-collected soil. Subsequent captures of juveniles could be due to reproduction in the soil trays (Table 4.2). Initial captures of Symphypleona, namely *S. elegans, Bourletiella hortensis* Fitch, and *S. viridis,* were predominantly of juveniles. This suggests that these species had been present as eggs or immatures in the overwintering soil samples (Table 4.2); no immature Collembola were found in searches through the newly collected field soil suggesting that these symphypleonids were present as eggs. No significant differences in the capture numbers were found between the soils from the two fields for most of the species hatched (*S. elegans* $F_{1,7} = 0.12$, $P > 0.05$; *S. viridis* $F_{1,7} = 1.16$, $P > 0.05$; all Symphypleona $F_{1,7} = 0.68$, $P > 0.05$; all Arthropleona $F_{1,7} = 0.96$, $P > 0.05$), suggesting that these two fields contained a similar epigeal collembolan fauna, except for *B. hortensis* ($F_{1,7} = 8.03$, $P < 0.05$).

B. hortensis was only found in the soil from one field. The very high numbers of *S. elegans* trapped over time suggest that this species may have been breeding successfully in the soil trays.

Table 4.2. Species found in or emerging from soil collected in the early spring from two arable fields in Hampshire. Soils were incubated under laboratory conditions. The total catch numbers from both soils is shown consisting of adults (A) and juveniles (J).

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

Following the four-month period of simulated drought, the soil trays were watered again. Fig. 4.2a shows that despite having been present in the soils immediately after collection, no Arthropleona (*Isotomurus* spp. or *I. viridis)* were caught after the drought. Only Symphypleona were captured after the drought, the majority being *S. elegans.* The catches of these two groups differed significantly overall ($F_{1,16} = 141.8$, $P < 0.001$), with symphypleonids being more numerous. *S. elegans* was trapped before and after the drought

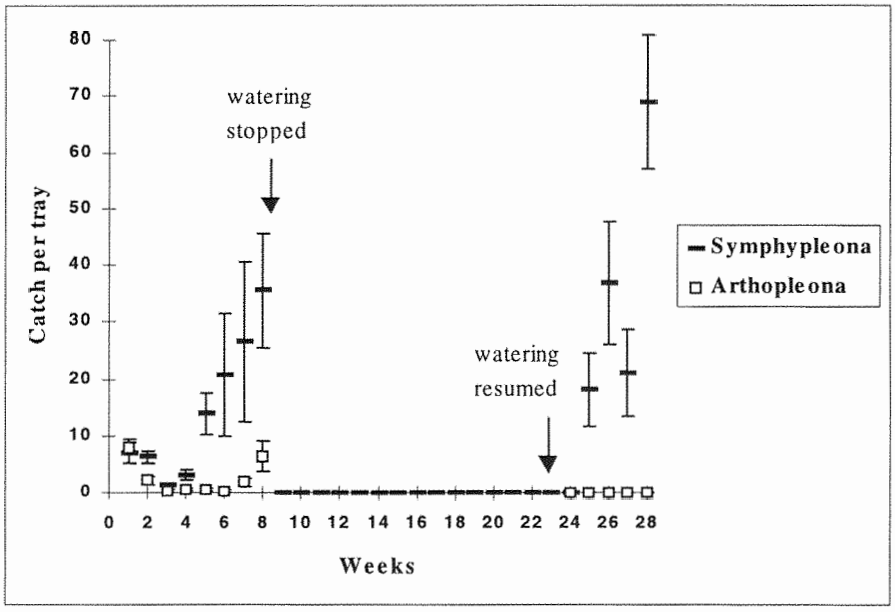
period (Fig. 4.2b); only juveniles were caught in the first samples post-watering. Other species of Symphypleona for which juveniles were captured included *B. hortensis* and *S. viridis*; other juveniles which were captured could not be accurately identified but comprised less than 5 % of the catch.

4.4.3 Species emerging under different rainfall simulation treatments

The dry soils collected from a field exposed to early spring drought which were subjected to different watering regimes produced very clear results in the first six weeks. Only the soils which were watered had surface-active Collembola present, and the highest catch occurred under the maximum rainfall treatment (Fig. 4.3a, 4.3b). Only Symphypleona were captured. The most common species caught was *S. elegans* (Fig. 4.3a), and significant differences were found between the treatments with the greatest catch occurring under the maximum rainfall treatment ($F_{2,12} = 72.8$, $P < 0.001$). Samples from the first week were composed wholly of juveniles whilst later samples comprised a mixture of adults and juveniles. No anhydrobiotic juveniles were found in the dry soil samples prior to watering, so the immature individuals which emerged can be assumed to have hatched from eggs. Desiccated adults of *Lepidocyrtus* spp. were found, but these are unlikely to have been viable as none were caught in the traps detecting surface activity. Other Collembola emerged but the juveniles could not be accurately identified and none were captured as adults. They are included here as 'all other Collembola' (Fig. 4.3b) and again significant differences were found in the catch means between the three rainfall treatments ($F_{2,12} = 21.4$, $P < 0.001$).

Figure 4.2. Overall emergence patterns of Collembola from two soils collected in the spring of 1996. Soils which were kept humid for the first eight weeks were allowed to dry out to simulate a four-month summer drought, after which watering was resumed. (a) Differences in hatching between Arthropleona and Symphypleona (mean number ± SE); (b) the emergence pattern of *S. elegans* (mean number ± SE).

a)



b)

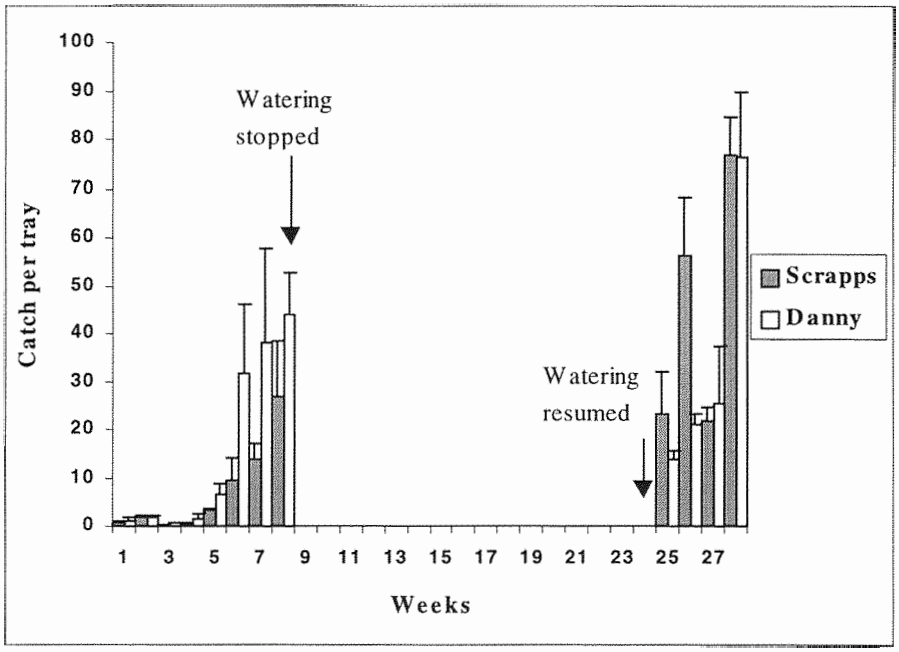
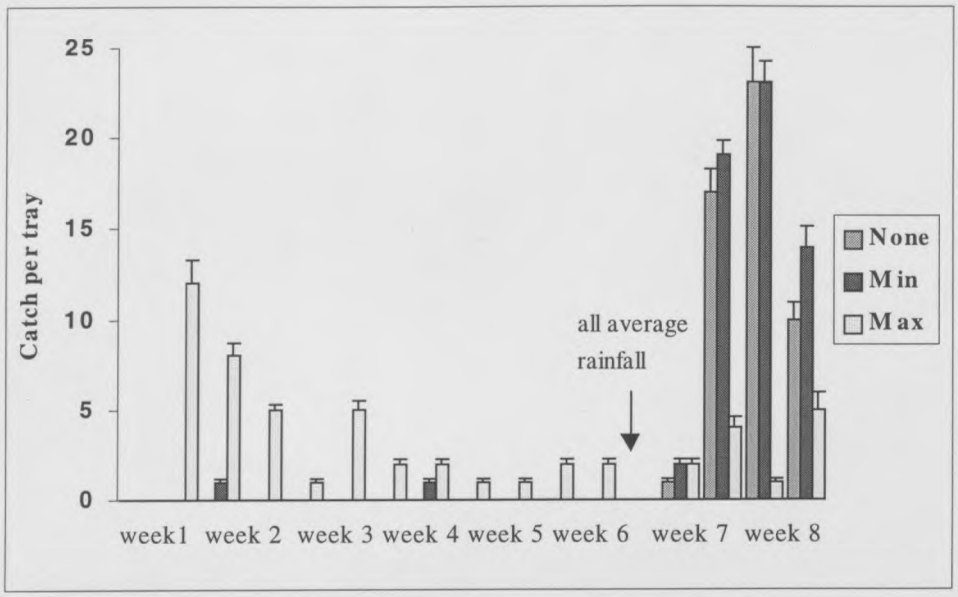
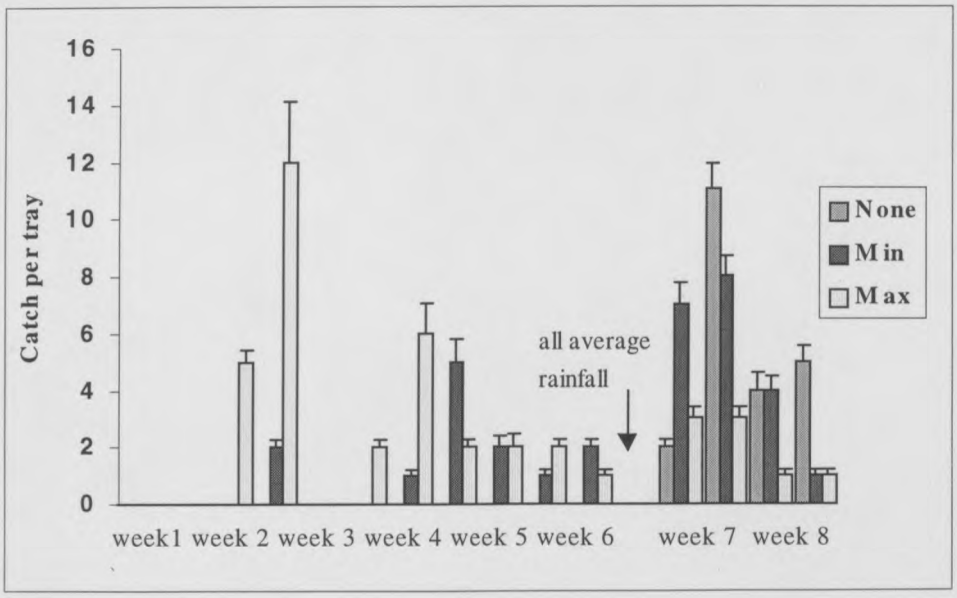


Figure 4.3. Emergence of Collembola from soils exposed to three simulated rainfall treatments during weeks 1-6. 'None' received no water; 'Min' received minimum rainfall equivalent to 1.9 mm per week; 'Max' received maximum rainfall equivalent to 23.7 mm per week. From week 7 all trays received the water volume equivalent to average rainfall. (a) Total number of adult and juvenile *S. elegans* caught in the emergence traps (mean number ± SE). (b) Total Collembola trapped excluding *S. elegans* (mean number ± SE).

a)



b)



The soils from all three levels of simulation rainfall treatments were subsequently supplied with the manipulated equivalent of average rainfall. Juveniles of *S. elegans* and other symphypleonids then emerged from the soils in all the trays (Fig. 4.3a, 4.3b), suggesting that the trigger for emergence was water availability as all other abiotic conditions were kept constant. Significant differences between the catch means from the different treatments were still found after this watering occasion (*S. elegans* $F_{2,12} = 6.5$, $P < 0.05$; other Symphypleona $F_{2,12} = 3.9$, $P < 0.05$). The lower number of individuals emerging from the maximum-rainfall trays at this stage was likely to have been due to a depletion in the desiccation-resistant population present in the soil, since emergence had been occurring in these trays from the beginning of the experiment.

4.5 Discussion

4.5.1 The development of an emergence trap

The detection of collembolan emergence from dry soils collected in the field then watered in the laboratory has only been carried out previously by Greenslade (1974, 1978). Her methods involved the extraction of Collembola from leaf litter using a Tullgren funnel and comparing the Collembola catch before and after watering leaf litter. Successive watering produced 'waves' of Collembola which were not obtained from the dry controls, which suggested that the hatching and activity of Collembola were triggered by water, and inactivated by dry conditions. However, this technique does not necessarily collect only the live Collembola from the sample, as dead individuals can be flushed out when the funnels are watered. It was therefore deemed necessary to develop a trapping system specifically

designed to capture active epigeal Collembola. The trap which I developed appeared to be effective in monitoring the presence and the hatching of Collembola from soils kept under controlled conditions. It is inexpensive and requires only basic equipment. It also allows manipulation of experimental conditions in order to ascertain triggering factors in the emergence rates of Collembola. The traps can be used for making direct comparisons between soils collected from diverse geographical locations and between different soil types. However there are limitations to this method:

(i) the disturbance of soils by sieving may be damaging to certain arthropods;

(ii) the humidity conditions produced by spraying the surface of the soil may favour some species above others;

(iii) the survival of newly hatched individuals may be affected by food availability. Conditions in the trays will affect the fungal community, which together with a lack of vegetation will help determine survival within the tray;

(iv) since the traps are water-filled, there may be a bias in catch towards those species which are hydrophilic.

This technique could also be used for the detection of other surface-active members of the mesofauna, such as the Acari: many mites were caught during the course of this investigation. As shown by the trapping efficiency experiment, the traps do not catch, and thereby remove, whole populations from the experimental chambers: since only a proportion of individuals are caught by the water traps, populations could survive in the containers. Long-term manipulation of microcosms in the soil trays could thus take place and the pitfall traps used to monitor their dynamics.

4.5.2 Implications of overwintering as eggs for pesticide exposure

Laboratory incubation of the soil collected from fields in March suggested that *I. viridis, Isotomurus* spp., and *Lepidocyrtus* spp. could have overwintered as adults. The Symphypleonids *S. elegans* and *S. viridis* probably overwintered as eggs as initial captures were predominantly of newly emerged juveniles. *S. viridis* is known to overwinter as eggs (Maclagan 1932a). Previous work has suggested that collembolan eggs are less sensitive to pesticides than adults or juveniles (Chernova *et al.* 1995), thus species which overwinter as eggs in the field may be less vulnerable to pesticide exposure than species which overwinter as adults. This has important implications for understanding non-target pesticide effects in the field, since previous work has suggested that wintertime exposure on the field when there is little or no crop cover together with a limited dispersal ability are the main factors explaining particularly detrimental effects to arthropod populations (Burn 1992).

4.5.3 Drought avoidance by arable field Collembola

These experiments gave an insight into the capacity of arable field Collembola to withstand drought. Whilst a four month period of drought in Britain has only occurred on rare occasions in the south of England, it is not uncommon in southern Europe. I used a four month early to late spring drought to represent a worst-case scenario for the Collembola in British arable fields.

Widely differing organisms including nematodes, rotifers and brine shrimps, have evolved ways of coping with extreme desiccation as a means of avoiding unfavourably dry conditions (Crowe *et al.* 1992, Sømme 1996). Many species of Collembola have evolved

desiccation-avoidance mechanisms in predictably dry environments, and their physiological basis is described by Poinsot-Balaguer & Barra (1991). Species adapted to periodic drought have been found in Australian and Mediterranean ecosystems (e.g. Greenslade 1973, 1981, 1985, Poinsot 1968, 1971, 1974, Vannier 1973), as well as in the Antarctic where desiccation occurs due to the extreme cold (Holmstrupp & Sømme 1998). In Australia the existence of 'resting' stages, i.e. diapause or anhydrobiosis, is well-recognised and taken into consideration when sampling in arid areas (e.g. Greenslade 1974, 1978). Some of these desiccation-resistant species are encountered in temperate European arable fields, in particular *Lepidocyrtus* spp. (Wood 1971), *Pseudosinella* spp. (Greenslade 1981), *Isotomurus* spp. (Poinsot 1971), *I. viridis* (Poinsot 1971), *I. notabilis* (Poinsot 1971), *Sminthurus aureus* Lubbock (Poinsot 1971), and *S. viridis* (Betsch-Pinot 1980).

My study found evidence for the existence of desiccation-resistant stages only in *S. viridis* amongst this list of Collembola. Other species which have previously been found aestivating did not hatch out under my experimental set-up despite being common in the fields from which the samples were taken (e.g. *Lepidocyrtus* spp., *Isotomurus* spp., *I. viridis*, *I. notabilis*, Chapter 2, Alvarez *et al.* 1997). Although drought-avoidance strategies are used by Collembola in more severe climate zones, there are few reports of drought resistance in temperate climates such as the UK (but see Blancquaert *et al.* 1981 for *S. aureus* and *S. pumilis*). Other species, which had not been previously reported to have drought-resistant eggs, were *S. elegans* and *B. hortensis*.

My results suggest that some of the symphypleonid Collembola of European arable fields have desiccation-resistant egg stages; no emergence occurred of arthropleonid species, which could be due to a lack of a resistant egg or juvenile stage. However this requires further testing, as under this experimental set-up other factors may have affected the presence of arthropleonid eggs including physical damage caused by the sieving of the soils, abiotic

conditions in the laboratory and the different phenologies of species such that egg stages may simply not have been present at the time samples were collected from the field. Future studies should investigate soils taken at different times of the year. Since my samples were taken in the early spring the eggs present were probably overwintering, but they are clearly also capable of surviving drought. In a recent review, Block (1996) suggested that drought tolerance mechanisms in arthropods could also pre-adapt them for tolerating freezing and *vice-versa*, since both factors involve desiccation. Hence overwintering populations of Collembola in the field could be less susceptible to drought than summer or autumn populations, a possibility which requires further investigation.

Previous work has suggested that several species of Symphypleona are better adapted to an epigeal lifestyle than most arthropleonids, by having morphological adaptations such as a primitive tracheal system and thicker integument. These have enabled them to colonise soil surfaces which are more climatically variable and drier than the soil itself (e.g. Davies 1928, Betsch & Vannier 1977, Betsch *et al.* 1980, Eisenbeis & Wichard 1987). The occurrence of aestivating eggs could also be considered as an adaptation to an epigeal lifestyle on the soil surface, where humidity gradients are less stable than underground. Further studies investigating the viability of drought-stressed eggs in relation to a variable egg moisture content could help to elucidate the responses by different species to dry conditions and hence their response to potential climate change.

The ability of some Collembola to survive through periods of desiccation has several implications. Desiccation tolerance may affect the dispersal capacities of these species. Dormant eggs could also be important sources of population recovery following the use of pesticides. There will also be implications for the effects of climatic change upon the northern European arable field fauna.

4.5.4 Implications for Collembolan dispersal.

Earlier in this century it was suggested that widely distributed collembolan species could be passively dispersed over substantial distances as an 'aerial plankton'(Glick 1939). Many authors have suggested that Collembola could be dispersed by air currents (e.g. see Hopkin 1997a and references therein), and indeed some springtails have been found in the air (Berland 1935, 1937, Freeman 1952). The widespread dispersal of certain Collembola species is undisputed, as can be seen from their capacity to colonise new islands (Christiansen & Bellinger 1995, and references therein). However, the high sensitivity to low humidity of most adult Collembola suggests that aerial dispersal could only be viable under high water saturation gradients, as were found in tropical conditions by Blackith and Disney (1988).

Certain species are able to withstand substantial desiccation as anhydrobiotic adults and these could provide a viable mechanism for dispersal. This was initially suggested by Murphy (1960), when he found that species which he described in Gambia (*Sminthurides ramosus* and *Sminthurus macrocerus)* also occurred in Hawaii and Costa Rica. He found that these species which live alongside ephemeral ponds had desiccation-resistant eggs in order to survive the periods of drought between rainfall events, and suggested that these could be picked up with dust by winds crossing the Atlantic. However this phenomenon has not been examined further in these species.

The ability of eggs to withstand desiccation could provide a more widespread mechanism, at least amongst the Symphypleona, by which Collembola could be passively dispersed by wind currents or on the feet of birds. More studies are required to evaluate the range of species which have drought-resistant egg stages, and the potential of these or of adult and juvenile anhydrobiotic stages as agents for passive dispersal.

4.5.5 Implications for studying pesticide non-target effects

Previous studies have suggested that the vulnerability to pesticides exhibited by Collembola makes them a good potential source of biological indicators to detect detrimental non-target effects of pesticide use (Filser *et al.* 1995, Frampton 1997b). However in order to be useful as biological indicators the species chosen should be spatially and temporally predictable. Since species vary in their resilience to adverse humidity conditions in the field, changes in the occurrence of droughts will alter species abundance and community composition.

Drought tolerance has been shown to be an important factor in determining the distribution of species in the field (e.g. Hertzberg & Leinaas 1998). Hence the species which are now sensitive to pesticide effects may not be useful in the future if climatic changes lead to altered annual phenologies, in turn affecting exposure to pesticides. In addition, climatic changes will cause other alterations in the management of arable fields, including planting, tillage and pesticide application times, all of which are known to affect populations of epigeal Collembola. Drought has also been show to exacerbate toxicity effects of pesticides upon Collembola in the laboratory (Holmstrupp 1997). This suggests that the sub-lethal effects of pesticides could be altered by the additional stress of desiccation, and would have implications for the collembolan communities in arable fields. This study suggests that some species may be better adapted to cope with changes in climate causing increased incidents of drought, and that these species should be considered in monitoring programmes for detecting pesticide non-target effects in future studies. This argument is also relevant to the use of Collembola for monitoring non-agricultural sources of pollution.

4.5.6 Effects of climatic change upon temperate arable field communities

Changes in abundance and in community composition could also affect ecosystem processes in the field. The majority of Collembola feed on fungi, so altering their grazing could have knock-on effects upon decomposition and levels of pathogenic fungi in the field. Collembola are important alternative prey for many beneficial predators used in IPM, so changes in their population levels could have an economically important impact by altering the dynamics within the food chain. Changes in collembolan abundance could thus have important implications for food webs in arable ecosystems, and alterations in collembolan community composition may be a useful monitoring tool for detecting the effects of climatic change.

4.6 Conclusions

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

5. The effects of organic, integrated and conventional farm management regimes upon epigeal Collembola in winter wheat

5.1 Summary

1. Community characteristics of Collembola assemblages in conventional, integrated and organic fields of winter wheat were compared among three randomly chosen areas in southern England. ANOVA and ANOSIM were used to compare measures of abundance and diversity among geographical areas and farming regimes. Cluster analysis and multidimensional scaling were used to identify similar fields and species assemblages. Indicator Values were used to identify indicator species.

2. Significant differences were found in the abundance of most species and in community structure among the three geographical regions. However, no differences were found in the diversity measures among the different areas and no species were found to be indicative of geographical region. At a local scale collembolan abundance was highly variable among fields.

3. Despite a lack of significant differences among regimes, two trends in population abundance were noticeable for individual species and taxa. *Entomobrya multifasciata* and *Isotomurus* spp. were consistently more common in conventional than organic fields; the opposite was true for *Isotoma viridis* and *Isotoma notabilis*. Farming regime significantly affected the abundance of *Sminthurinus elegans* and *Sminthurus viridis* but the effect differed among regions. Community composition and species dominance were affected by differences in farming regime, but no species were indicative of differences in farming regime as most were ubiquitous.

4. Organically and conventionally farmed fields were found not to differ significantly from each other in community composition, but both differed from integrated fields.

Significant differences in sample similarities among the three regimes were also found by ANOSIM.

5. These findings are compared with the results from other recent European studies of the impact of farming systems on arthropods and their wider ecological implications are discussed.

5.2 Introduction

Previous studies investigating the invertebrate fauna of fields managed under organic, conventional and integrated regimes have reported significant differences in faunal diversity. Several studies have reported positive effects upon species diversity and population abundance in low-input and organically managed fields compared to conventional management. A higher diversity of species and taxa, and a higher equitability, have been found in organically cultivated fields for Carabidae (e.g. Kromp 1989, 1990), spiders and Carabidae (Steinborn & Meyer 1994), Collembola (Paoletti *et al.* 1992), and a variety of beneficial arthropods (El Titi & Ipach 1989, Moreby *et al.* 1994, Drinkwater *et al.* 1995, Reddersen 1997). Positive effects of low-input (but not organic) systems have been reported on earthworms (Steiner *et al.* 1986), Carabidae and spiders (Steiner *et al.* 1986, Ulber *et al.* 1990), soil microarthropods (Siepel 1996), and soil invertebrates (Bardgett & Cook 1998). Increased biotic diversity has been associated with greater ecosystem stability and sustainability (Seastedt 1984, Bardgett & Cook 1998). Such potential ecological benefits have been highlighted in support of organic farming for conservation purposes (e.g. Drinkwater *et al.* 1995).

Results of farming systems studies have, however, not always been consistent. A greater abundance and diversity of carabid beetles was found in conventional than organic fields by Armstrong (1995), perhaps because mechanical weed control disturbed faunal populations in the organic fields. Foissner (1992) found that climate and farm type were more important than management regime as determinants of species presence and abundance of earthworms, nematodes and protozoa.

Collembola are among the most abundant of farmland arthropods, and contribute both to the arthropod food web (e.g. Hopkin 1997a) and to decomposition and soil nutrient dynamics (e.g. Petersen & Luxton 1982, Kiss & Jager 1987, Mebes & Filser 1998). Some species of Collembola are vulnerable to the pesticides used under conventional farming practices (e.g. Reddersen 1995, van Straalen & van Rijn 1998, Frampton 1999) so a potential exists for pesticide-mediated differences in collembolan abundance between farming systems. In organic regimes no pesticides are allowed except for restricted use of copper- or sulphur-based fungicides (Lampkin 1992). Under an integrated regime pesticide use is minimised: generally insecticides are avoided and the main inputs comprise herbicides and fungicides. Conventional farming regimes use insecticides, herbicides and fungicides according to need as determined by individual farmers.

Relatively few studies have investigated variation in collembolan abundance between farming systems and none have so far investigated the effects of management practices upon collembolan diversity and community composition. Paoletti *et al.* (1992) and Moreby *et al.* (1994) found a greater abundance of Collembola in organic than conventional cereals, but in the latter case only in one year of a two-year study. Steiner *et al.* (1986) found a greater abundance of Collembola in integrated than in conventional fields of cereals and sugar beet. However, no significant differences were found in collembolan abundance between organic

and conventional fields in large-scale regional studies carried out on various arable crops (Dekkers *et al.* 1994, Czarnecki & Paprocki 1997) or in cereals (Reddersen 1997).

Given the inconsistencies of results obtained from previous work, the present study focused on one crop type (winter wheat). The aim was to compare collembolan presence, abundance and community measurements in arable fields at different spatial scales under differing farming regimes to determine whether any species, species assemblages, or community parameters are characteristic of particular farming systems. Conventional farms were used to represent high levels of pesticide use, integrated farms provided a low pesticide input comparison and organic farms supplied a no-pesticide situation.

5.3 Methods

5.3.1 Study area and experimental design

Organic farms were randomly selected from the list of certified organic growers in southern England. Certification requires a minimum of two years without pesticide use prior to organic approval (Lampkin 1992) so all the organic crops sampled had experienced at least three years without pesticide use. Conventional and integrated farms were chosen to be within 25 km of the organic ones. Two research farms, CWS Agriculture (Leicestershire, 52° 40' N, 1° 0' W) and Rhone-Poulenc's Boarded Barns Farm ('BB', Essex, 51° 30' N, 0° 20' W) were included in this study to permit within-farm sampling of neighbouring fields managed under conventional, organic and integrated regimes. A total of 24 fields were included in this study, in three areas of southern England (Fig. 5.1, Table 5.1). Fields in adjacent regional groups of farms (Wiltshire and Hampshire; Essex and Berkshire) were considered together for analysis.

No pesticides were used in organic fields, except for an application of sulphur as a fungicide at BB (sulphur is not known to have detrimental effects upon Collembola although it could affect their fungal food availability). None of the insecticide inputs into the integrated or conventional fields (cypermethrin or pirimicarb; Table 5.1) are known to be toxic to Collembola (Wiles & Frampton 1996). The inputs in the conventional fields were representative of conventional pesticide use in fields of winter wheat in the UK (Thomas 1997).

Figure 5.1 Locations of the farms sampled in this study.

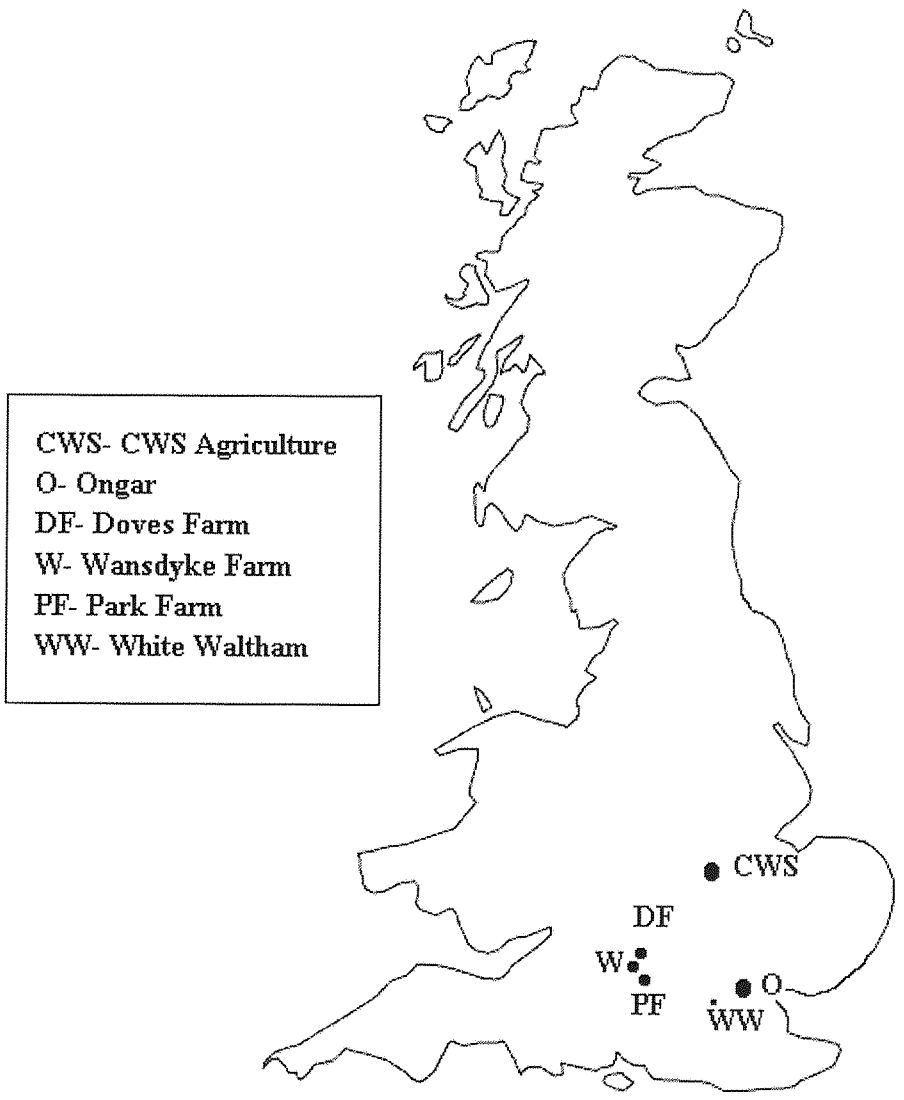


Table 5.1 Characteristics of the organic (org), conventional (con) and integrated (int) fields investigated in this study. All fields contained winter wheat sown in autumn 1996. For field edges H = hedgerow, F= arable field, W = woods, T = track or road, G = grass bank. NA = information not available. * Growth stage on sampling date (Tottman 1987).

Regime	Location	Number of fields	Average field size (ha)	Soil type	Cultivar, growth stage*	Sampling date	Field edges	Pesticide inputs?
Org	Stoughton (CWS Agriculture) (52° 40' N, 1° 0' W)	3	12	Medium to heavy clay loam	NA; g.s.64-65	17/6/97	HHFF HHWW HHFW	None
Org	White Waltham (White Waltham) (51° 20' N, 0° 30' W)	2	2.0	Medium loam on flinty clay	NA; g.s.64-65	24/6/97	HHWF	None
Org	Ongar (Boarded Barns) (51° 30' N, 0° 20' W)	1	2.6	Medium loam over chalky boulder clay	Hereward; g.s. 64-65	10/6/97	HHHG	Sulphur as a fungicide
Org	Heckfield (Park Farm) (51° 0' N, 1° 10' W)	1	14.9	Medium loam on chalky clay	NA; g.s.60-61	9/6/97	HHFW	None
Org	Ham (Doves Farm) (51° 40' N, 1° 30' W)	2	9.6	Chalky flinty clay	NA; g.s.64-69	16/6/97	HHFT	None
Int	Stoughton (CWS Agriculture) (52° 40' N, 1° 0' W)	3	4.5	Medium to heavy clay loam	Hunter, Reaper, Hussar; g.s.64-65	17/6/97	HFWW HHFT	Herbicides: Glyphosate, isoproturon, fenoxyprop-P-ethyl, metsulfuron-methyl, fluroylycoen-ethyl Fungicides: cyproconazole, prochloraz, epoxiconazole, fenpropidin Growth regulators: chlormequat

Table 5.1 continued...

Regime	Location	Number of fields	Average field size (ha)	Soil type	Cultivar, growth stage	Sampling date	Field edges	Pesticide inputs?
int	Ongar (Boarded Barns) (51° 30' N, 0° 20' W)	3	3.9	Medium loam over chalky boulder clay	Spark, Rialto, Hunter g.s.64-65	10/6/97	HHHT HHFF	Herbicides: Isoproturon, diflufenican, mecoprop-P Fungicides: tebuconazole & triadimenol, propiconazole, chlorothalonil Insecticides: cypermethrin, fenpropathrin Growth regulators: chlormequat
Con	Stoughton (CWS Agriculture) (52° 40' N, 1° 0' W)	3	4.4	Medium to heavy clay loam	Hunter, Reaper, Brigadier; g.s.64-65	19/6/97	HHHF HHFT	Herbicides: Isoproturon, diflufenican, glyphosate, fluroglycofen-ethyl Fungicides: cyproconazole, prochloraz, fenpropidin, propiconazole, tebuconazole, kresoxim-methyl, fenpropimorph, epoxiconazole, difenoconazole, quinoxyfen, Insecticides: cypermethrin Growth regulators: chlormequat, 2-choloroethylphosphonic acid
con	Ongar (Boarded Barns) (51° 30' N, 0° 20' W)	2	3.8	Medium loam over chalky boulder clay	Rialto; g.s.64-65	10/6/97	HHHF HHFF	Herbicides: glyphosate, isoproturon, diflufenican, mecoprop-P, Fungicides: chlorothalonil, tebuconazole & triadimenol Insecticides: cypermethrin, pirimicarb Growth regulators: chlormequat
con	Ham (Wansdyke Farms) (51° 40' N, 1°30' W)	4	12	Chalky flinty clay	NA; g.s. 64-68	16/6/97	HHHT HHHF HHHH	NA

5.3.2 Collembola sampling

Suction sampling was carried out using a leaf-blower (Ryobi RSV3100) adapted as described in Stewart & Wright (1995). Samples were taken 30 m from the nearest hedgerow and more than 50 m away from any other field edge. Four suction samples were taken at random from each field. For each sample a total area of 0.5 m^2 was sampled, comprising five pooled sub-samples each of 10-s duration. All sampling took place between the 9 June and 24 June 1997.

Samples were frozen within three hours of collection. Collembola were later separated by floatation in water and sieving (3 μm mesh) then transferred into 80% methylated spirit. Species were examined using binocular and compound light microscopes. The most common species were initially identified with Stach (1947, 1956, 1963), verified with Fjellberg (1980) and Christiansen & Bellinger (1980, 1998). In order to investigate diversity among the treatments, rare species were assigned to operational taxonomic units (OTU's - Hopkin 1997a, 1997b) for which type specimens were held.

5.3.3 Univariate statistical analysis

Collembolan abundance, number of species, and several different indices of diversity were examined. Shannon-Wiener diversity, Pielou's evenness, Margaleff species richness and Simpson's measure of dominance were all obtained using the programme DIVERSE available in PRIMER (Plymouth Routines in Multivariate Ecological Research ©1994 Plymouth Marine Laboratory). All calculations for analysis of variance were carried out using EXCEL (©1985-1997 Microsoft Corporation) and SPSS (©SPSS Inc. 1989-1997). The $\log_{10}$

(x + 1) transformed data for species catch, and the untransformed data for species diversity measures, were tested for heterogeneity of variance using Cochran's test (Underwood 1997) and for departure from normality using the Kolmogorov-Smirnov test (Sokal & Rohlf 1995). Where data fulfilled requirements for parametric analysis, analysis was carried out using ANOVA to look at treatment differences due to pesticide regime (fixed factor), regional area (random factor) and field (random factor) nested within regime and area. The general linear model used was:

$$X_{arfn} = \mu + \rho_r + A_a + \rho A_{ra} + F(\rho A)_{f(ar)} + e_{arfn}$$

Subscripts stand for: a = area, r = regime, f = field, and n = replicate 'n'. X_{arfn} is thus the measure of variation for the n^{th} replicate in a given combination of regime, area, and field nested within regime by area interaction. The sources of variation come from μ, the overall mean of all populations being sampled; ρ_r the variation component due to regime; A_a the variation component due to area; ρA_{ra} is the interaction term for regime by area; $F(\rho A)_{f(ar)}$ denotes the variation due to field, which is nested within the area by regime interaction; and finally the error, or residual, component of variation is denoted by e_{arfn} (see Underwood 1997 for a general review on nested ANOVA).

A lack of integrated farms in Wiltshire and Hampshire (Table 5.1) precluded a fully balanced design so two separate ANOVAs were carried out: (1) organic fields were compared to conventionally managed fields in three areas; (2) the variation among all three farming regimes was compared but using farms only in Leicestershire and Berkshire. A missing conventional field replicate from the Berkshire group was substituted in analyses with the mean count data from the other eight conventional fields; the loss in variance was

compensated for by adjusting the degrees of freedom used to test the F-value (Underwood 1997).

Differences among regimes in measures of overall diversity and abundance were compared using a 1-way ANOVA. Species compositions among regimes were compared using a linear regression on relative abundance against rank number of species. The regression slopes for each farming regime were compared using t-tests for each pairwise comparison (Fowler & Cohen 1992). Since multiple tests were carried out, Bonferroni methods were used to adjust the significance level in the t-tests to reduce the likelihood of Type I errors (Sokal & Rohlf 1995).

5.3.4 Multivariate analysis

Multivariate analysis was carried out to investigate the complex community data and was complementary to univariate analysis (see Gauch 1982, Jongman *et al.* 1987 for general reviews). These techniques are useful for representing communities in two-dimensional space and testing for differences in community composition. Hierarchical agglomerative cluster analysis, multi-dimensional scaling (MDS) and 2-way crossed analysis of similarities (ANOSIM) were carried out on $\log_{10}(x+1)$ transformed means (for simplification, and since replicates within a field were used to estimate the population of that field, the field mean abundance for each species was used in this analysis) in order to group fields containing similar communities. Bray-Curtis coefficients of similarity (Bray & Curtis 1957), were used to produce similarity matrices. The $\log_{10}(x+1)$ transformation was used to down-weight the importance of the very abundant species (Gauch 1982, Jongman *et al.* 1987) since the data for Collembola abundance tends to be widely spread. Analysis of the species similarity matrix

was used to identify species assemblages. Rare species, where they contributed less than 1% to the total abundance, were omitted from species similarity analysis. Presence/absence data for all species was also used for community comparisons.

For the non-metric MDS which was carried out to rank the similarities between samples and/or species, the accuracy was tested by measuring the goodness of fit of a non-parametric regression of distances on the MDS plot, against Bray-Curtis similarity measures (Clarke & Warwick 1994). An iterative procedure was carried out and the most frequently occurring ordination with the best fit (i.e. the minimum stress value) was plotted as the most accurate representation of field and species groupings.

Dendrogram results of cluster analysis were compared to the results from MDS ordination to verify their accuracy in distinguishing groups. Groupings from the clustering dendrogram are shown as circles upon the MDS plots for different levels of similarity. Species indicative of the different groupings were identified using species indicator values (INDVAL; Dufrêne & Legendre 1997).

ANOSIM was carried out on the fields' similarity matrices to test whether there were differences in community composition according to the groups defined *a priori* according to different agricultural regimes and geographical areas. A 2-way crossed design was used to produce a test statistic, R, of differences between groups compared to differences within groups. The level of significance associated with these differences was tested using a general randomisation-permutation approach to generate significance levels (Monte Carlo tests - see Clarke & Warwick 1994).

5.4 Results

5.4.1 Species abundance

The most common species encountered were: *Lepidocyrtus* spp., *Pseudosinella alba* (Packard), *Sminthurinus elegans* (Fitch), *Sminthurus viridis* (L.), *Isotomurus* spp., *Isotoma viridis* Bourlet, *I. notabilis* Schäffer, and *Entomobrya multifasciata* (Tullberg). A substantial amount of variation was found to occur among the three geographical areas investigated, but the most important source of variation was between fields at a local scale. Consistently significant differences were found between fields for all the common species investigated (Tables 5.2 and 5.3).

Table 5.2 Differences in individual species counts between organic and conventional fields sampled in three areas (Leicestershire, Berkshire and Wiltshire). Significant results (3-way nested ANOVA) are denoted by * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

Species	Regime	Area	Regime × Area	Field
Lepidocyrtus spp.	$F_{1,2}$=1.48 NS	$F_{2,11}$=2.22 NS	$F_{2,11}$=0.32 NS	**$F_{11,51}$=16.46*** **
S. elegans	$F_{1,2}$=0.06 NS	**$F_{2,11}$=7.94****	**$F_{2,11}$=4.31***	**$F_{11,51}$=9.98*** **
I. viridis	$F_{1,2}$=10.48 NS	**$F_{2,11}$=5.65***	$F_{2,11}$=0.10 NS	**$F_{11,51}$=24.42*** **
E. multifasciata	$F_{1,2}$=4.06 NS	$F_{2,11}$=0.28 NS	$F_{2,11}$=1.18 NS	**$F_{11,51}$=10.60*** **
Isotomurus spp.	$F_{1,2}$=0.77 NS	**$F_{2,11}$=25.13*** **	$F_{2,11}$=2.61 NS	**$F_{11,51}$=11.15*** **
I. notabilis	$F_{1,2}$=0.29 NS	**$F_{2,11}$=5.34***	$F_{2,11}$=1.21 NS	**$F_{11,51}$=13.45*** **
S. viridis	$F_{1,2}$=0.10 NS	$F_{2,11}$=1.03 NS	**$F_{2,11}$=4.92***	**$F_{11,51}$=14.41*** **
P. alba	$F_{1,2}$=0.02 NS	$F_{2,11}$=3.25 NS	$F_{2,11}$=0.43 NS	**$F_{11,51}$=18.63*** **

Table 5.3 Differences in individual species abundance between Berkshire and Leicestershire in fields managed under organic, integrated or conventional regimes. Significant results (3-way ANOVA) are denoted by * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

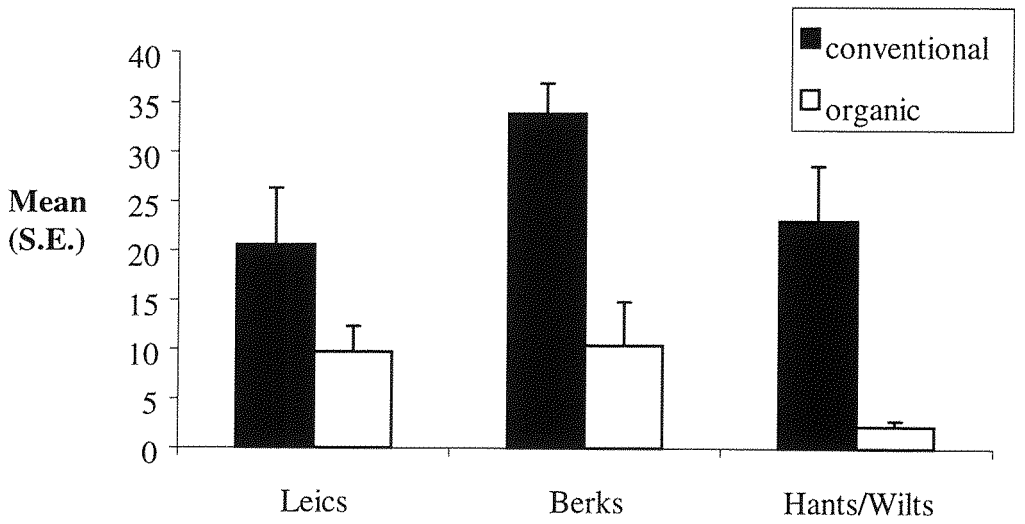
Species	Regime	Area	Regime × Area	Field
Lepidocyrtus spp.	$F_{2,2}$=0.37 NS	**$F_{1,11}$=8.49****	$F_{2,11}$ =3.61 NS	**$F_{11,51}$=16.79*****
S. elegans	$F_{2,2}$=0.14 NS	**$F_{1,11}$=11.55****	**$F_{2,11}$ =5.31***	**$F_{11,51}$=19.09*****
I. viridis	$F_{2,2}$=9.31 NS	**$F_{1,11}$=9.14***	$F_{2,11}$ =0.39 NS	**$F_{11,51}$=11.76*****
E. multifasciata	$F_{2,2}$=4.52 NS	$F_{1,11}$=0.45 NS	$F_{2,11}$ =0.78 NS	**$F_{11,51}$=18.73*****
Isotomurus spp.	$F_{2,2}$=10.48 NS	**$F_{1,11}$=57.94*****	$F_{2,11}$ =0.74 NS	**$F_{11,51}$=15.40*****
I. notabilis	$F_{2,2}$=3.59 NS	**$F_{1,11}$ =9.56****	$F_{2,11}$ =1.23 NS	**$F_{11,51}$=14.47*****
S. viridis	$F_{2,2}$ =0.38 NS	$F_{1,11}$ =1.75 NS	**$F_{2,11}$ = 5.15***	**$F_{11,51}$=9.39*****
P. alba	$F_{2,2}$=0.01 NS	$F_{1,11}$ =0.08 NS	$F_{2,11}$ =0.88 NS	**$F_{11,51}$=6.82*****

Four different trends in the abundance of lower taxa were evident: (1) *E. multifasciata* and *Isotomurus* spp. were consistently more common in conventionally than organically managed fields in all three areas (Fig. 5.2a, 5.2b), and *E. multifasciata* was most numerous in integrated fields. (2) *I. viridis* and *I. notabilis* were consistently although not significantly more numerous in organic than conventional fields (Fig. 5.3a, 5.3b). (3) *S. elegans* and *S. viridis* showed a significant interaction between regime and area indicating that differences among regimes were not consistent at all geographical locations (Fig. 5.4a, 5.4b). For both of these species few differences were found in counts between organic and conventional fields in Hampshire and Berkshire; however populations were much higher in conventionally managed fields than organically managed fields in Leicestershire. (4) *Lepidocyrtus* spp., *I.*

viridis, Isotomurus spp. and *I. notabilis* all differed significantly in abundance between Leicestershire and Berkshire (Table 5.3).

Figure 5.2 Differences in the abundance of (a) *E. multifasciata* and *(b) Isotomurus* spp. between fields farmed organically and conventionally in three areas. Mean abundance did not differ significantly among regimes (Table 5.3). Count = mean abundance/field.

a) *E. multifasciata*



b) *Isotomurus spp.*

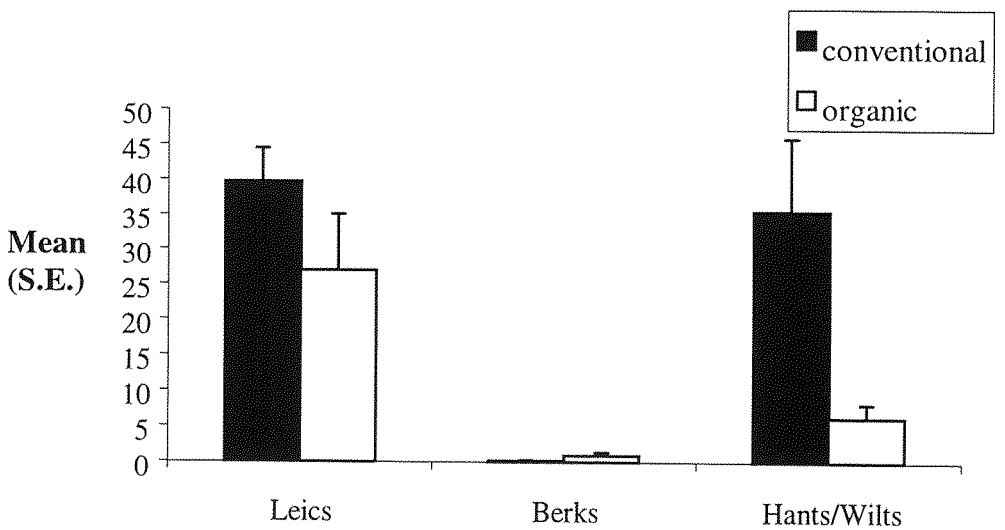
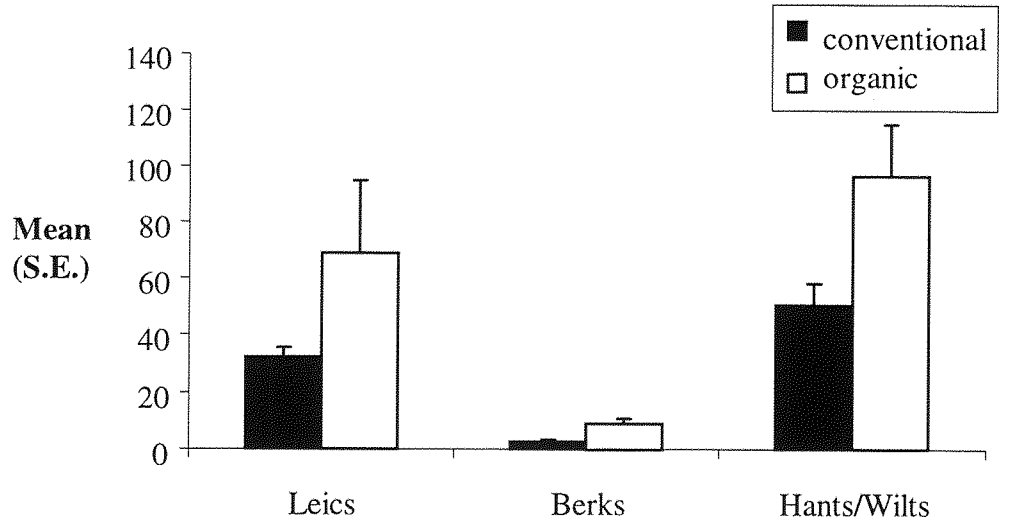


Figure 5.3 Differences in the abundance of (a) *I. viridis* and *(b) I. notabilis* between fields farmed organically and conventionally in three areas. Mean abundance did not differ significantly between regimes (Table 5.3). Count = mean abundance/field.



b) *I. notabilis*

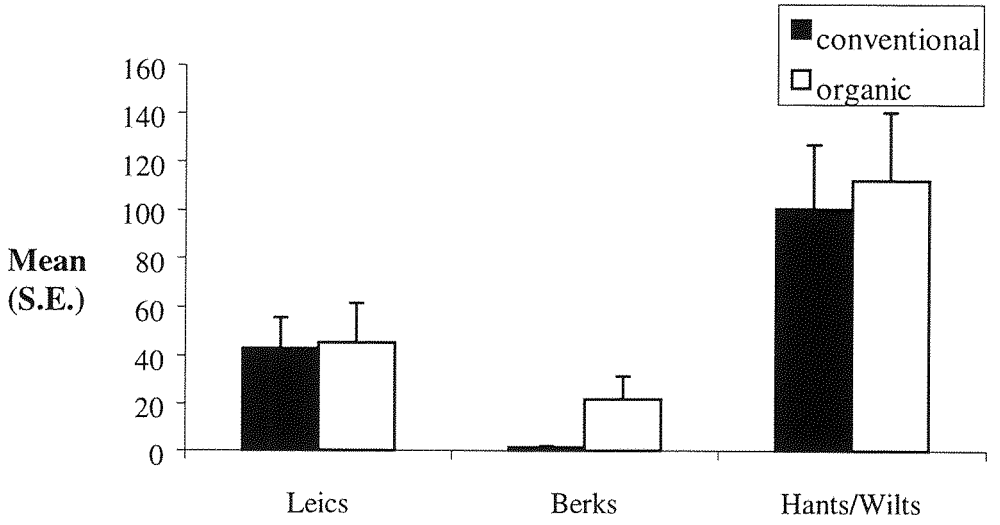
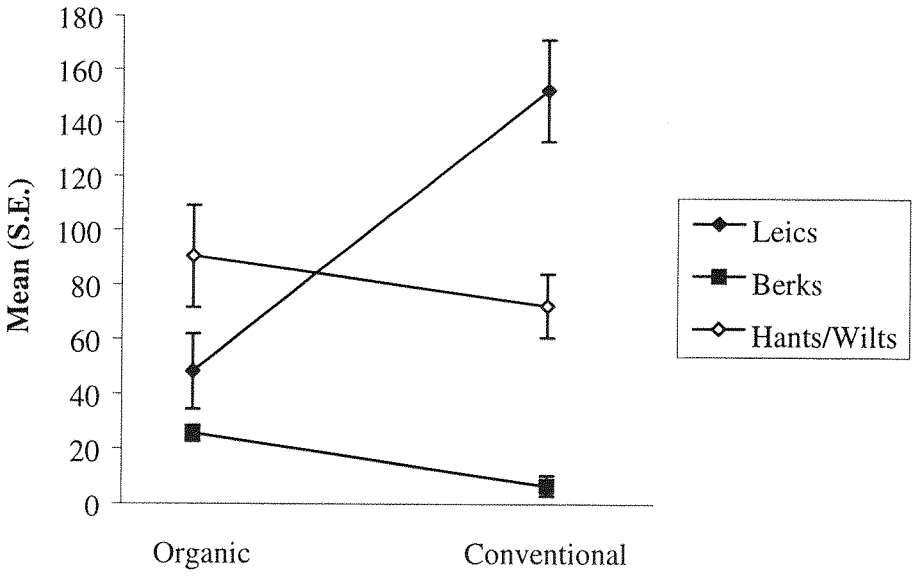
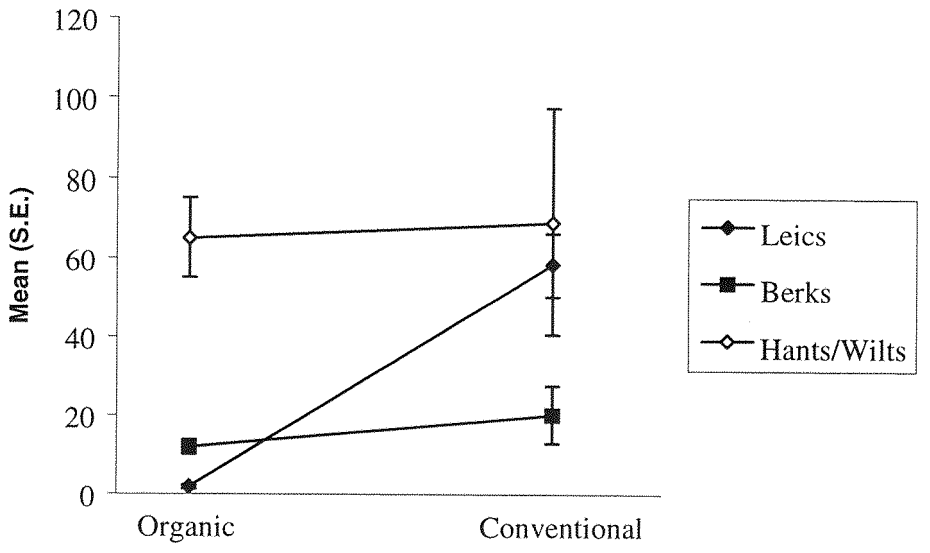


Figure 5.4 Interaction plots for regime (organic and conventional) and region for (a) *S. elegans* and (b) *S. viridis*.

a) *S. elegans*



b) *S. viridis*



5.4.2 Community parameters

As with the lower taxa, major differences in overall collembolan abundance and diversity counts were found at a local, (i.e. field) scale (Tables 5.4 and 5.5). Only dominance differed among regimes. Dominance differed significantly among regimes (Table 5.4), the highest values being found in fields farmed organically (mean = 0.28, SE = 0.01) compared to those farmed conventionally (mean = 0.26, SE = 0.01) or under an integrated regime (mean = 0.25, SE = 0.01). Symphypleona abundance differed between regimes but inconsistently between different areas. Total counts of Arthropleona and Collembola differed significantly among geographical regions but not management regimes. No significant differences were found in species richness, diversity and evenness measures due to either regime or area (Tables 5.4 and 5.5).

Table 5.4 Differences in overall abundance and diversity measures for Collembola counts between organic and conventional regimes sampled in three areas (Leicestershire, Berkshire and Wiltshire). Significant results (3-way ANOVA) are denoted by * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

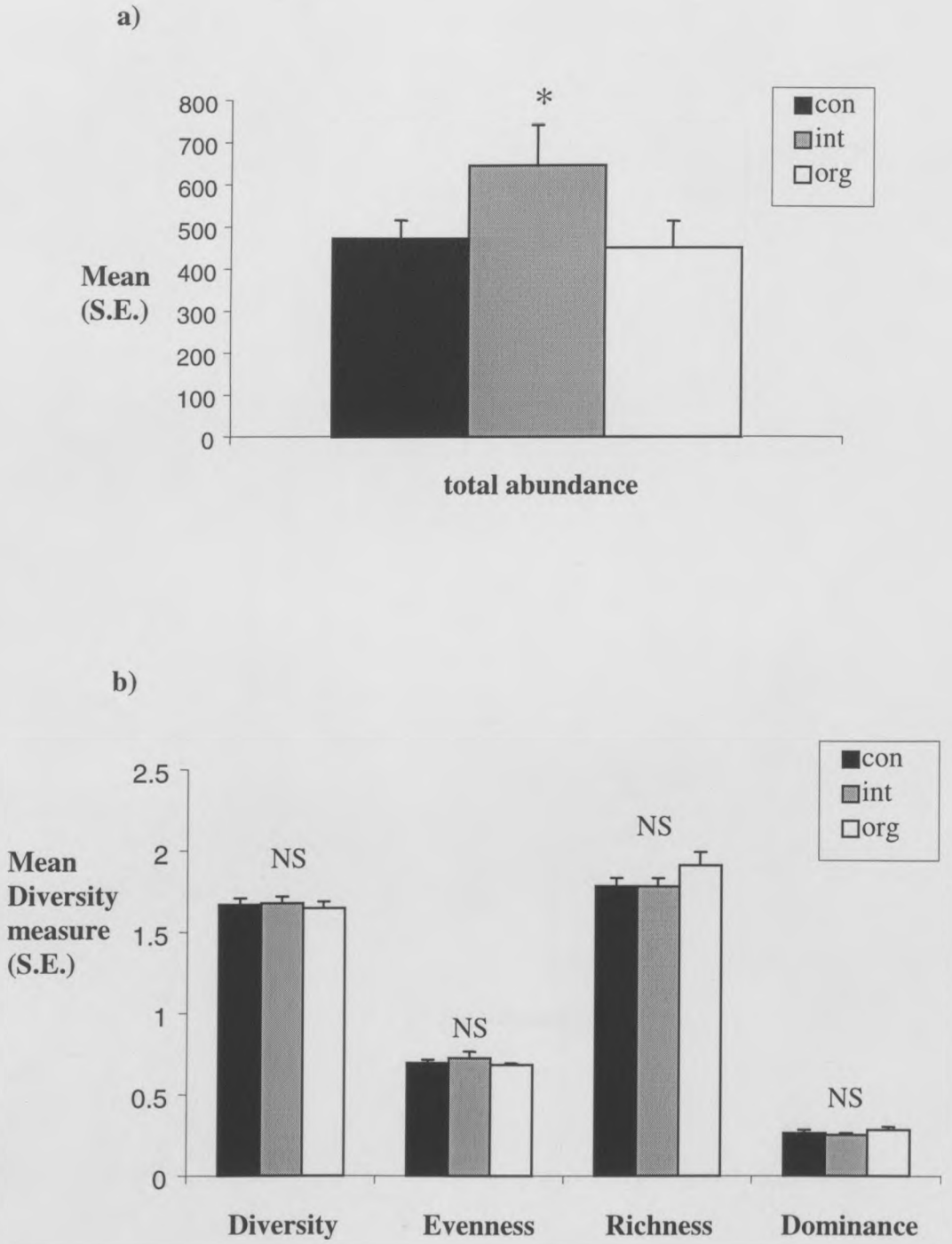
Measure	Regime	Area	Regime × Area	Field
Total Symphypleona	$F_{1,2}$ = 0.002 NS	**$F_{2,11}$ = 3.85***	**$F_{2,11}$ = 4.06***	**$F_{11,51}$=14.38*****
Total Arthropleona	$F_{1,2}$ = 0.24 NS	**$F_{2,11}$ = 5.72***	$F_{2,11}$ =0.19 NS	**$F_{11,51}$=17.64*****
Total Collembola	$F_{1,2}$ = 0.07 NS	**$F_{2,11}$ = 6.93***	$F_{2,11}$ = 0.74 NS	**$F_{11,51}$=15.76*****
Total species number	$F_{1,2}$ = 0.58 NS	$F_{2,11}$ = 2.85 NS	$F_{2,11}$ = 0.38 NS	**$F_{11,51}$ =8.47*****
Richness	$F_{1,2}$ = 2.29	$F_{2,11}$ = 0.37 NS	$F_{2,11}$ = 0.29 NS	**$F_{11,51}$=16.93*****
Diversity	$F_{1,2}$ = 2.69 NS	$F_{2,11}$ = 0.58 NS	$F_{2,11}$ = 0.10 NS	**$F_{11,51}$=16.93*****
Evenness	$F_{1,2}$ = 11.81 NS	$F_{2,11}$ = 0.16 NS	$F_{2,11}$ = 0.09 NS	**$F_{11,51}$ =7.78*****
Dominance	**$F_{1,2}$ = 19.7***	$F_{2,11}$ = 0.43 NS	$F_{2,11}$ =0.06 NS	**$F_{11,51}$=13.43*****

Table 5.5 Differences in overall abundance and diversity measures for Collembola counts between Leicestershire and Berkshire in fields managed under organic, conventional or integrated regimes. Significant results (3-way ANOVA) are denoted by * = P < 0.05, ** = P < 0.01 *** = P < 0.001.

Species	Regime	Area	Regime x Area	Field
Total Symphypleona	$F_{2,2}$ =0.13 NS	**$F_{1,11}$ =5.24***	**$F_{2,11}$ =5.40***	**$F_{11,51}$=12.36*****
Total Arthropleona	$F_{2,2}$ =6.82 NS	**$F_{1,11}$ =8.31***	$F_{2,11}$ =0.70 NS	**$F_{11,51}$=19.55*****
Total Collembola	$F_{2,2}$ =2.97 NS	**$F_{1,11}$ =16.18****	$F_{2,11}$ =1.17 NS	**$F_{11,51}$=13.91*****
Total species number	$F_{2,2}$ =2.69 NS	**$F_{1,11}$ =11.75****	$F_{2,11}$ =0.42 NS	**$F_{11,51}$=4.84*****
Richness	$F_{2,2}$ =12.80	$F_{1,11}$ =0.73 NS	$F_{2,11}$ =0.07 NS	**$F_{11,51}$=7.67*****
Diversity	$F_{2,2}$ =3.84 NS	$F_{1,11}$ =1.17 NS	$F_{2,11}$ =0.01 NS	**$F_{11,51}$=12.61*****
Evenness	$F_{2,2}$ =0.77 NS	$F_{1,11}$ =0.01 NS	$F_{2,11}$ =0.54 NS	$F_{11,51}$=1.58 NS
Dominance	**$F_{2,2}$ =26.16***	$F_{1,11}$ =0.89 NS	$F_{2,11}$ =0.03 NS	**$F_{11,51}$=11.51*****

When only comparing overall regime effects (i.e. irrespective of regional differences; 1-way ANOVA), total collembolan abundance differed significantly, with the highest abundance occurring under integrated management (Fig. 5.5a). No other measures of diversity differed significantly between farming regimes (Fig. 5.5b).

Figure 5.5 Overall comparison of community measures for Collembola caught in fields managed under organic (org), conventional (con) or integrated (int) regimes. (a) Total collembolan abundance; (b) measures of diversity. Significant differences (1-way ANOVA) are denoted by * = P < 0.05, NS = no significant difference.



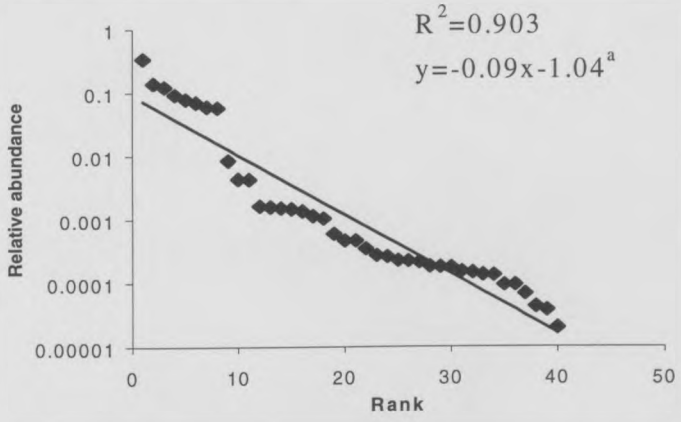
Differences in community composition were found between geographical areas and between regimes using ANOSIM (Table 5.6), however this technique does not show where the differences are. The regression slopes for rank-abundance plots differed significantly among regimes (Fig. 5.6). Slopes of the linear regressions for catches in conventional and organic fields did not differ significantly from each other (Bonferonni significance level for a 5% experiment-wise error rate is 0.017; $t_{73} = 2.37$, $P > 0.017$). However both conventional ($t_{65}=7.23$, $P<0.01$) and organic ($t_{62} = 6.85$, $P < 0.01$) fields differed from integrated fields. *E. multifasciata*, *I. viridis*, *I. notabilis* and *Isotomurus* spp. made up 70% of the total collembolan abundance in integrated fields (respectively 20%, 20%, 15% and 15%). In organic and conventional fields the community was dominated by *Lepidocyrtus* spp. (respectively 28% and 34%).

Table 5.6 Differences in collembolan communities among three agricultural management regimes and three areas in southern England: results of 2-way ANOSIM.

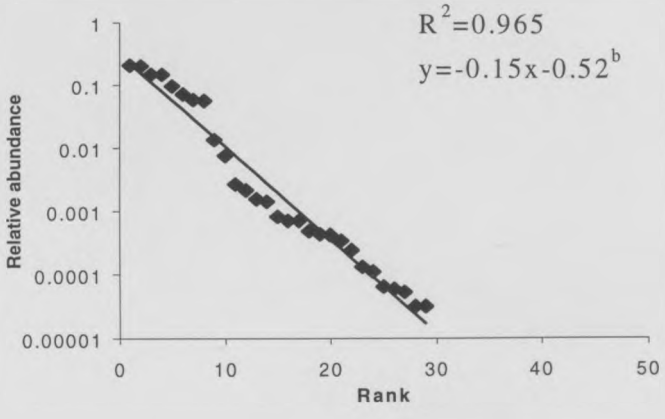
Details of comparison	Test statistic R	Significance level
Log(x+1) transformation, abundance data for all species:		
Regimes: organic v. conventional	R=0.469	**0.008**
Areas: all 3 areas	R=0.588	**0.001**
Regimes: all 3 regimes	R=0.593	**0.0001**
Areas: Leicestershire v. Berkshire	R=0.753	**0.001**
Presence/absence data for all species:		
Regimes: Organic v. conventional	R=0.296	**0.022**
Areas: all 3 areas	R=0.374	**0.011**
Regimes: all 3 regimes	R=0.451	**0.0001**
Areas: Leicestershire v. Berkshire	R=0.630	**0.001**

Figure 5.6 Rank-abundance plots for species trapped in (a) conventional, (b) integrated and (c) organic fields. Slopes for regimes with different suffixes differ significantly (t-test; P <0.05). Each point on the graph represents an individual species or operational taxonomic unit.

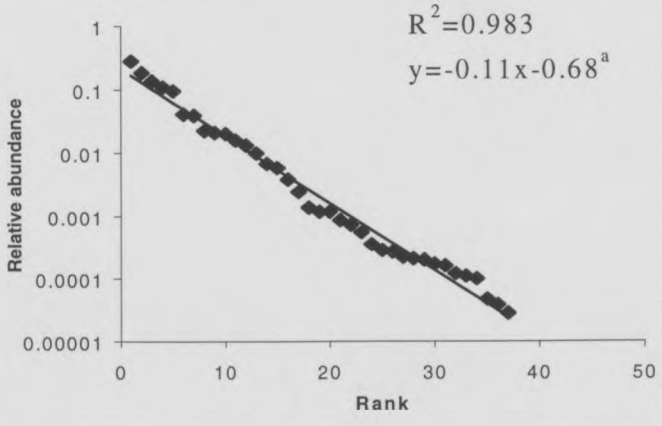
a) Conventional



b) Integrated



c) Organic



Cluster analysis grouped species together which were widespread and abundant. The main group comprised *Lepidocyrtus* spp., *S. elegans, I. viridis, E. multifasciata, Isotomurus* spp., *I. notabilis, S. viridis* and *Deuterosminthurus* spp. Rarer species showed no relationship to other species' patterns of abundance (Fig. 5.7, Fig. 5.8).

MDS analysis of the species composition in the samples from each field grouped fields together which were farmed under the same regime in the same area (Fig. 5.9, Fig. 5.10). However, species indicator values (Dufrêne & Legendre 1997) showed that no species or groups of species were indicative of the groupings produced by MDS and cluster analysis. All numerous species had their highest INDVAL value when the whole data set was treated as one group, suggesting that these species are ubiquitous in all the arable systems investigated; rare species did not differ in abundance from a random distribution among samples.

Figure 5.7 Species groupings found by Multi-Dimensional Scaling upon the species similarity matrix (mean abundance data). Groups are delineated according to the results of cluster analysis. MDS stress = 0.17. The dashed line groups samples on a basis of > 45% similarity, the black line groups samples on a basis of > 30% similarity.

LC= *Lepidocyrtus* spp.; SE= *S. elegans;* OD=*Deuterosminthurus* spp.; IV=*I. viridis;* EM=*E. multifasciata;* IP= *Istomurus* spp.; IN= *I. notabilis;* SV= *S. viridis;* PA= *P. alba;* EN= *E. nicoleti;* LL= *L. lignorum*; HN= *H. nitidus;* OV= *O. villosa;* O1= *Orchesella* operational taxonomic unit (OTU); GP & PP= Poduroidea OTU's; S1,S2 & S3= Symphypleonid OTU's; BW= Isotomid OTU.

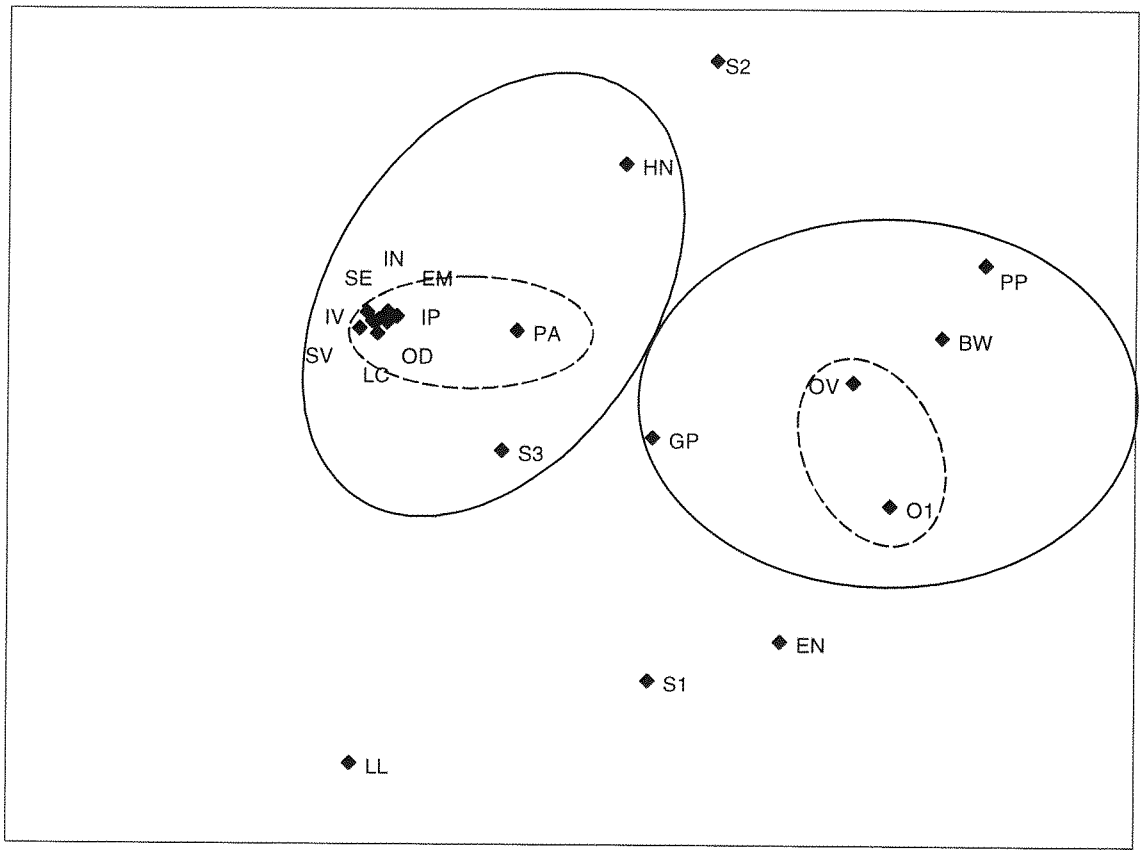


Figure 5.8 Species groupings found by Multi-Dimensional Scaling analysis upon the sample similarity matrix (presence and absence data). Groups are delineated according to the results of cluster analysis. MDS stress=0.17. The dashed line groups samples on a basis of > 70% similarity, the black line groups samples on a basis of > 40% similarity. (Symbols as in Fig. 5.7).

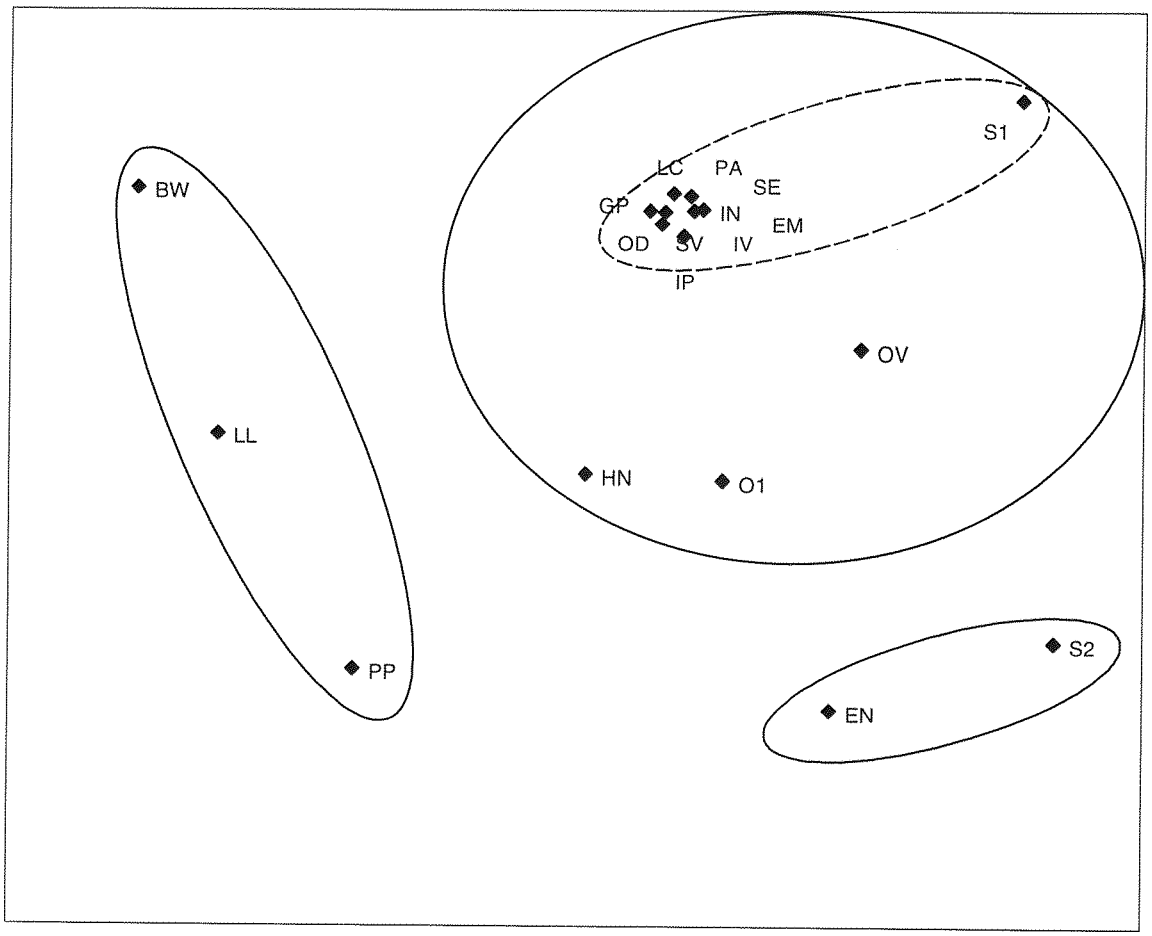


Figure 5.9 Field groupings found by Multi-Dimensional Scaling analysis upon the sample similarity matrix (mean abundance data). Groups are delineated according to the results of cluster analysis. MDS stress=0.12. The dashed line groups samples on a basis of > 70% similarity, the black line groups samples on a basis of > 65% similarity. Numbers 1-3 refer to areas (1=Leicestershire, 2=Berkshire, 3=Wiltshire/Hampshire). Letters refer to farming regime (or= organic, co= conventional, in= integrated).

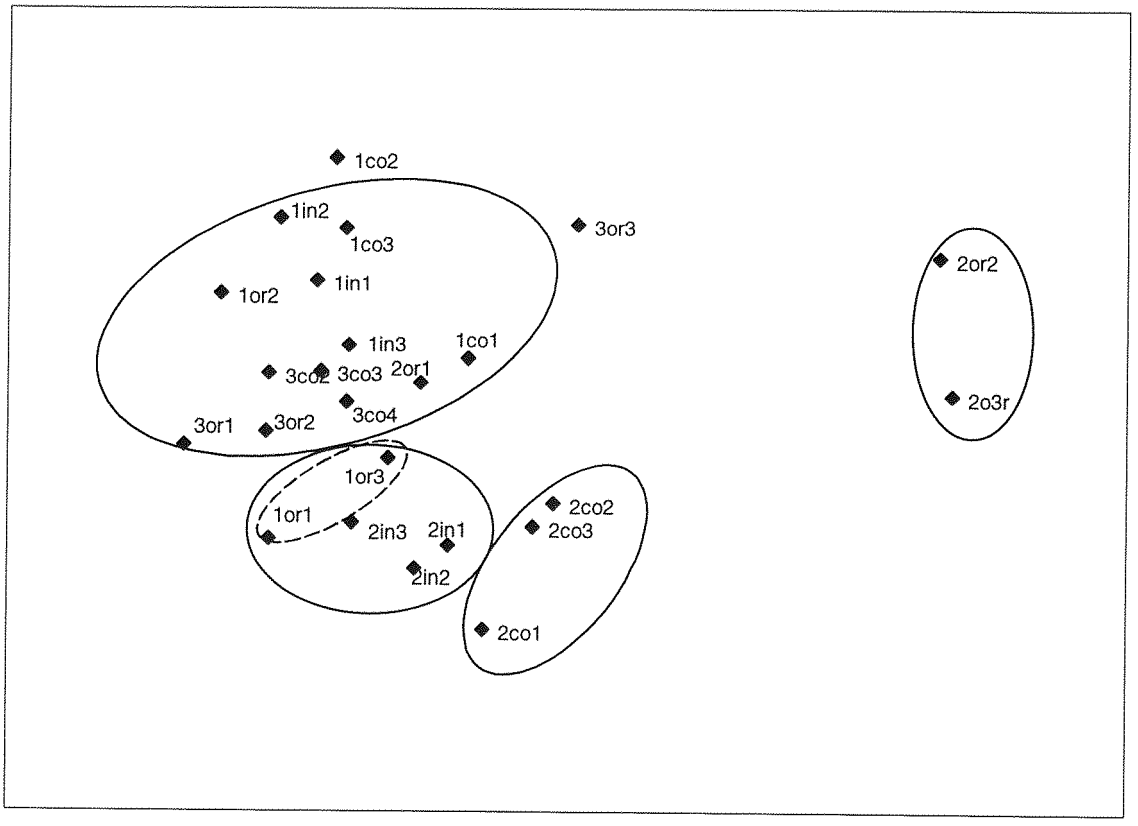
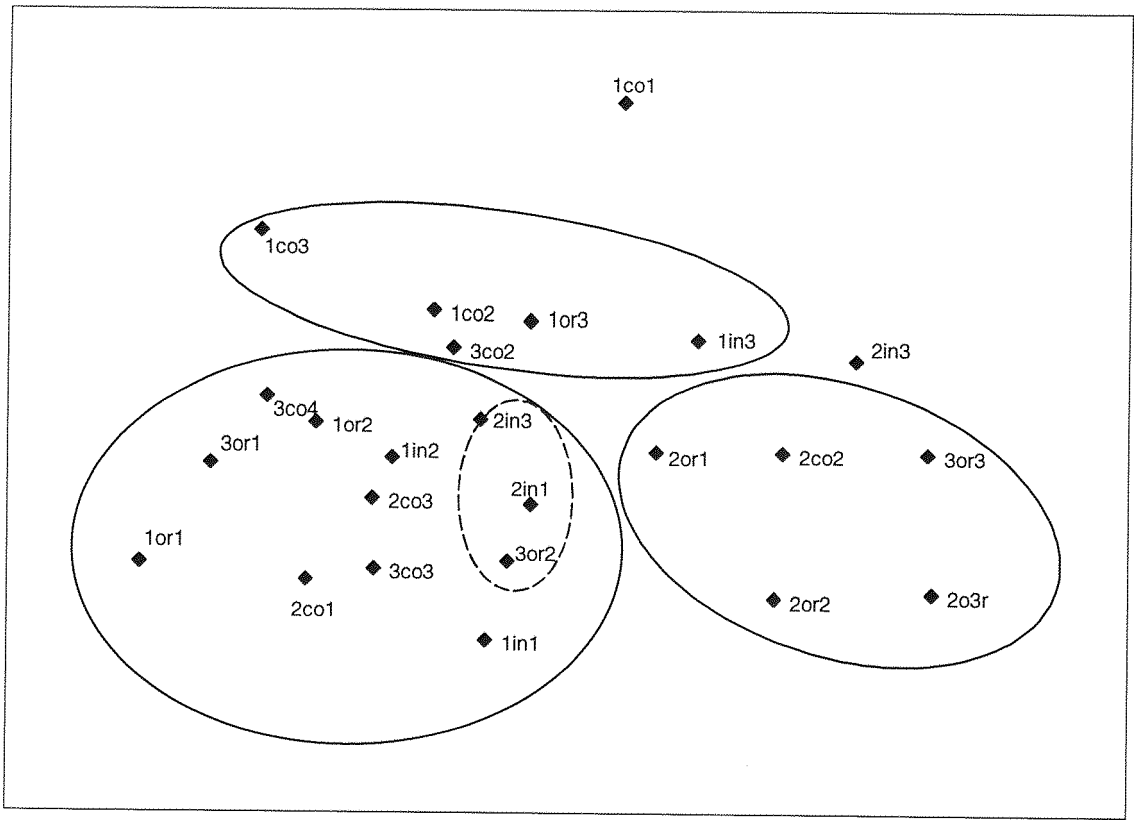


Figure 5.10 Field groupings found by Multi-Dimensional Scaling analysis upon the sample similarity matrix (presence and absence data). Groups are delineated according to the results of cluster analysis. MDS stress=0.18. The dashed line groups samples on a basis of > 70% similarity, the black line groups samples on a basis of > 65% similarity. Symbols as in Fig. 5.9.



5.5 Discussion

5.5.1 Differences in species abundance

E. multifasciata, Isotomurus spp. and *I. notabilis*, total Arthropleona and total Collembola were all most abundant under integrated management. As previously mentioned, the major differences between integrated and conventional fields usually lie in their relative use of pesticides, particularly insecticides, and in tillage practices. During the sampling for this study, however, integrated farming systems did not differ from conventional ones in the use of insecticides: both used pirimicarb which is known not to be harmful to Collembola (Cole & Wilkinson 1985, Wiles & Frampton 1996). Thus differences in collembolan abundance between integrated and conventional fields could be due to either the use of other inputs (more fungicides were used in conventional fields and these are known to affect Collembola - Frampton 1989), or to previous use of pesticides in the fields investigated. Organophophorus compounds in particular are known to cause long-term reductions in the populations of some Collembola (Frampton 1997b). Further information on cropping histories could help to determine whether this was the case.

Alternatively, Collembola populations are known to be reduced by soil disturbance, in particular the deep ploughing and heavy machinery use (Heisler 1991, Kracht & Schrader 1997) which are more common under conventional farming practices (Locke & Bryson 1997). Conservation tillage is frequently used in integrated farming (Locke & Bryson 1997) and this could explain the high arthropod abundance in integrated fields. Further studies would be required to differentiate the causes of differences between integrated and other farming regimes. Likewise, further information is necessary to determine why certain species

were more common in integrated fields than in organic fields, since both of these regimes use soil conservation tillage techniques.

A consistently and significantly higher abundance of *E. multifasciata* and *Isotomurus* spp. was recorded in conventional fields than in organic fields. These differences could be due to these species being less vulnerable to pesticide effects under field conditions than other Collembola. However, previous studies have found that *E. multifasciata* is detrimentally affected by the application of some pesticides (Frampton 1997b). Alternatively, this species is known to be tolerant of dry conditions (Davies 1928), which could occur in conventionally farmed fields where herbicide use reduces weed cover increasing water loss by evaporation (Moreby *et al.* 1994). A third explanation could be that this species may be highly mobile and able to recolonise disturbed fields quickly, however this is contrary to previous findings (Frampton 1997a). Any of these scenarios would provide *E. multifasciata* with a competitive advantage in the collembolan community under conventional farming conditions. Further studies on direct pesticide effects, desiccation resistance and dispersive capabilities influencing competitive exclusion within collembolan communities could help determine the mechanisms responsible for the higher populations of this taxa in conventionally farmed fields.

In accordance with Prasse (1985), the opposite pattern occurred in populations of *I. viridis* and *I. notabilis* and in the total counts for Arthropleona. In this case consistently, but not always significantly, higher counts were found in organically farmed fields compared to conventionally farmed fields. Both of these species, together with *P. alba* and *S. elegans*, are known to be detrimentally affected by herbicide use (Prasse 1985). The sensitivity of *I. viridis* to insecticide applications has been used for studying pesticide effects in laboratory and semi-field tests (Wiles & Frampton 1996, Wiles & Krogh 1998). Alternatively, both *I. viridis* and *I. notabilis* are known to require high humidity (Davies 1928) and hence could be put at a

competitive disadvantage if herbicide use reduces ground cover and decreases humidity at ground level.

S. viridis was also found to be consistently but not significantly more common in organic fields than in conventional fields. This species is well adapted to an epigeal lifestyle and able to withstand drier environments than *I. viridis* and *I. notabilis* (Davies 1928). It is also known to be sensitive to some pesticides (e.g. Wallace 1959, Gimeno & Perdiguer 1995, Wiles & Frampton 1996, Bishop *et al.* 1998). Its abundance in organic fields could be explained by feeding habits: since *S. viridis* is herbivorous its abundance could be favoured by the high level of weediness experienced in organic fields (Moreby *et al.* 1994). Similarly, high weediness could also explain the higher overall counts of Symphypleona in organic systems in Leicestershire and Wiltshire (no weed counts were made in this study but the organic fields were noted to be weedier than conventional or integrated fields).

Despite the ubiquitous nature of the common Collembola which were identified, considerable variations were found in species abundance among regions. Higher numbers of Collembola were found in conventional fields in Hampshire compared to fields managed under the same regime in both Leicestershire and Berkshire. Berkshire had the lowest population abundance for all species (except *E. multifasciata*), and also had the lowest number of species per sample. The differences in abundance between the three regions investigated are likely to reflect variations caused by differences in local climate and soil type. For the purposes of ecological monitoring of regime effects, the high regional variation in abundance is problematic. Studies are unlikely to detect regime differences unless they are planned within strictly delineated geographical scales. The distances over which comparisons can detect differences require further investigation. This regional-scale variation may help to explain the different results produced by studies on different scales comparing organic and conventional collembolan faunas. For example, the large-scale study carried out by Reddersen

(1997) found no differences in collembolan abundance among regimes, in contrast to the smaller-scale study carried out by Moreby *et al.* (1994) which found significant differences between the regimes.

5.5.2 Differences in community composition

In common with Prasse (1985), differences were found in community composition between agricultural regimes. The communities in integrated fields were less equitable and less speciose than those found under either of the other two regimes. This pattern of high abundance for a few species is associated with highly stressed environments (Begon *et al.* 1990), however it is not clear why fields farmed under an integrated regime should be more disturbed than either organic or conventional fields. Both organic and conventional fields showed a more equitable species distribution than integrated fields, although the data showed that about 30% of total abundance was due to one taxon (*Lepidocyrtus* spp.) in both conventional and organic fields. No support was found for organic fields having a greater diversity than other farming regimes. However the most equitable community structure was found under organic farming, in agreement with Steinborn & Meyer (1994). Community equitability has been linked to ecosystem resilience and hence to its sustainability (Naeem *et al.* 1995).

The differences in community composition and equitability were however not demonstrated using species diversity measures, suggesting they may not be ideal for detecting community level effects. Many criticisms have been made of the use of diversity measures (e.g. Cousins 1991, Cairns *et al.* 1993) and multivariate analytical techniques are generally accepted as a better approach for detecting pollutant effects (see Cairns *et al.* 1993, Cao *et al.*

1996 for general reviews). In comparisons made among multivariate techniques, MDS in particular was found to provide the clearest spatial separation of community structure, although unlike DCA it does not indicate species importance (Cao *et al.* 1996). In this study the ordination techniques did not show any clear differences in groups among the regimes, however the use of ANOSIM demonstrated significant differences according to regime. In conjunction with the rank-abundance plots, different patterns were discernible but should be treated with caution as these were produced on the whole data set without taking into account regional differences.

5.5.3 Limitations of the study

The extent of this study was limited by the amount of sampling that could be carried out and by the availability of suitable fields. Ideally fields should have been matched according to inputs and soil type as well as crop cover; however this was impractical due to the small number of organic fields available for investigation. Other sources of variation known to affect collembolan populations include previous crops, tillage, and pesticide history. In future studies including these variables in a multivariate investigation could help to elucidate the role of management regime in determining collembolan species abundance.

The sampling scheme was designed to produce an estimate of the field populations, taking into account the spatial heterogeneity that has been previously observed for Collembola (see section 2.3.2, Frampton 1994). The results of this study showed that the majority of variation in species abundance and in overall measures of diversity occurred among fields. The high among-fields variation meant that differences due to regime or area were unlikely to be detected using standard parametric techniques, unless replication of fields

was increased. This field to field variation was also notable in the results from cluster analysis and MDS ordination: some regional differentiation occurred, but generally no pattern emerged in the faunal similarity between fields.

Few previous studies have explicitly investigated variation in Collembola populations between agricultural fields. This study has shown that such variability needs to be taken into account in further investigations, and replication taken at appropriate spatial scales to be more likely to detect differences, if any are present, among farming regimes. Heterogeneity among fields would be expected due to differences in moisture (e.g. Joosse & Groen 1970), food availability (e.g. Christiansen 1970) and soil type (Kovac 1994) as well as aspects of soil management including tillage (Kracht & Schrader 1997, Heisler & Brunotte 1998). Further studies could measure these variables and include them in multivariate analysis in order to distinguish pesticide regime from other environmental and management factors. In addition, the temporal predictability of collembolan species requires further investigation. Previous work suggests a high variability (e.g. see Bengtsson 1994, Reddersen 1997, Moreby *et al.* 1994) and appropriate sampling scales should also be established for future studies.

5.6 Conclusions

Three different agricultural management regimes were investigated in this study. The regimes were chosen to represent systems using decreasing quantities of pesticides: from conventional, through integrated, to organic farming which allows no pesticide inputs. However, other factors which are known to detrimentally affect collembolan populations also varied between these management regimes. These would have included the intensity and frequency of tillage (Heisler 1994b), different crop covers (Chapter 2, Alvarez *et al.* 1997,

Dekkers *et al.* 1994), and fertilizer and nutrient inputs (Sievers & Ulber 1990b, Filser 1995a). These differences may have obscured any effects of pesticide use.

Several species were found to be ubiquitous in presence but their populations did not vary significantly according to differences in farming regime. This study agrees with most of the existing literature that farming regime is not a major determinant of epigeal arable Collembola populations. Overall, the pattern emerging is one of high variability at local spatial scales. Within-field variability is well known in the literature, however the importance of variation at a landscape level between fields has been less well recognised. Kovac & Miklisova (1997) also encountered the high level of variation that occurs between fields.

Despite the limitations of this study, especially with regard to the distances between 'matched' fields, consistent patterns were detected in the abundance of different species in fields farmed under the three management regimes.

6. General Discussion

6.1 Summary

Aspects of the ecology of epigeal Collembola in arable fields in the UK were investigated in order to provide information on the mechanisms of exposure to, and recovery from, pesticide use. This information could contribute towards an explanation for previous observations that some species are particularly vulnerable. Responses of Collembola to different farm management practices and their possible use as ecological indicators of farming system were also investigated.

In the current work, some species were closely associated with hedgerows whilst others were present predominantly in open fields (Table 6.1, Chapters 2, 3). Populations of several species or genera were present within fields over winter (Table 6.1, Chapter 2). These comprised *Lepidocyrtus* spp., *B. hortensis*, *I. viridis*, and *Isotomurus* spp. Such Collembola could be at increased risk of exposure to winter pesticide sprays when little protective crop cover is present. Species which overwintered as eggs in open fields (*S. elegans*, *S. viridis*; Table 6.1, Chapter 4) could be less vulnerable by escaping exposure to winter pesticide applications.

Some species of Collembola (*S. elegans*, *S. viridis*, *I. viridis*) were found to disperse into arable fields from an adjacent hedgerow, providing the first evidence that hedgerows may be important sources for collembolan colonisation of arable fields, or recolonisation following disturbances due to pesticide applications or tillage (Table 6.1, Chapter 3).

Table 6.1 Aspects of ecology found during the current work which could affect collembolan exposure to, and potential for recovery from, pesticide applications. The information presented is for species proposed as potential ecological indicators (Frampton 1994, 1997b). Numbers refer to the chapter in which the results were presented. N.S. = no significant differences found among the results of treatments; * = no drought resistant stage was found in this study despite previous reports of drought resistance (see Chapter 4 for details and references).

Species	Temporal distribution	Spatial distribution	Crop effects	Potential sources of recovery	Drought resistant form	Differences among agricultural regimes
S. elegans	Rare as overwintering adults (2) but present as eggs (4), common in spring & summer (2)	Common throughout fields (2), especially field edges (3)	Differed between crops, more abundant in peas than barley (2)	Hedgerows (3), eggs within field soils (4)	Eggs (4)	Significant interaction between region and farming regime (5)
S. viridis	Rare as overwintering adults (2) but present as eggs (4), common in spring & summer (2)	Common throughout fields (2) especially away from edges (3)	Differed between crops, more abundant in barley than peas (2)	Hedgerows (3), eggs within field soils (4)	Eggs (4)	Significant interaction between region and farming regime (5)
B. hortensis	Overwintered as adults, rare in spring & summer (2)	Common near field edges (2, 3)	No difference found (2)	Eggs within field soils (4)	Eggs (4)	No consistent difference found (5)
I. viridis	Overwintered as adults, common in spring (2)	Common near field edges (2); also found common away from edges (3)	Differed between crops, more abundant in peas than barley (2)	Hedgerows (3)	None found (4)*	More abundant in organic than conventional fields (5) Differ among regions (5)
I. notabilis	Overwintered as adults, rare in spring (2)	Common near edges (3)	No difference found (2)	Unknown	None found (4)*	More abundant in organic than conventional fields (5) Differed among regions (5)

Table 6.1 continued...

Species	Temporal distribution	Spatial distribution	Crop effects	Potential sources of recovery	Drought resistant form	Differences among agricultural regimes
Isotomurus spp.	Overwintered as adults, rare throughout the study period (2)	Common near edges (2, 3)	No difference found (2)	Within field from unknown source (3)	None found (4)*	More abundant in conventional than organic fields (5) Differed among regions (5)
E. multifasciata	Unknown overwintering strategy; common only in summer (2)	Common near edges (2, 3)	Differed between crops, more abundant in barley than peas (2)	Unknown	None found (4)	More abundant in conventional than organic fields (5)
Lepidocyrtus spp.	Overwintered as adults, common throughout the year (2,4)	Found throughout fields (2), especially away from edges (3)	Differed between crops, more abundant in peas than barley (2)	Within field from unknown source (3)	None found (4)*	Differed among regions (5)
P. alba	Unknown overwintering strategy; rare throughout the year (2)	Rare throughout fields (2, 3)	No difference found (2)	Unknown	None found (4)*	Differed among regions (5); only found in 1 area.

The current study also provided the first evidence that Collembola (*S. elegans, S. viridis, B. hortensis*) in northern European arable fields can survive at least four months under drought conditions. This is relevant to pesticide non-target effects, as some previous work has suggested that for Collembola the egg stage may be the least sensitive to pesticides. Increasingly warmer and drier conditions predicted for Britain are likely to favour collembolan species that are drought-resistant, with a potential impact on the community structure present in fields. The availability of vulnerable species for detecting pesticide effects

could therefore change. Little is known about the dispersive capacities of collembolan species on farmland landscape levels, and the existence of desiccation-resistant egg stages might be a viable mechanism for passive wind dispersal (Chapter 4).

In order to be suitable as ecological indicators, for example of non-target pesticide effects or farming systems, organisms should fulfil several requirements including sensitivity, amenability for sampling, and predictability in spatial and temporal distribution. Collembolan species abundance and community composition were compared in fields of winter wheat managed under organic, conventional and integrated farming regimes but no individual species or species assemblage was found to be characteristic of any one farming regime. However, community composition did vary among regimes and several species were consistently more abundant under conventional (e.g. *E. multifasciata*; Table 6.1), or under organic systems (e.g. *I. notabilis*; Table 6.1). The major source of variability in collembolan populations was attributable to the distribution between fields and regions, which has implications for the scales at which farming systems studies are conducted (Chapter 5).

6.2 Dispersal in Collembola

Very little is known about the dispersal ability of Collembola at the scale of agricultural fields, as the movement of epigeal species within or between fields has not been measured. Dispersal of edaphic species at small (micro- and mesocosm) scales has been investigated in laboratory studies and found to be very limited. At the other extreme, studies have investigated dispersal at landscape levels in non-agricultural habitats, but have focused only upon mass migration events which are probably rare, occur in only a few species, and only in unusual weather conditions (e.g. on snow-covered ground - Hågvar 1995). No study

has yet been carried out to investigate more generalised methods of landscape-scale dispersal which could be used by widely-distributed species of Collembola. Whilst passive means of dispersal have been attributed to wind, oceanic currents and phoresy, none of these have been proven to be widespread and, as discussed previously (section 1.6.2, Chapter 4), there is relatively little evidence in support of them.

Certain widespread Collembola (e.g. *I. viridis*, *I. notabilis*, *S. elegans*, *Lepidocyrtus cyaneus* and *L. violaceus*, *E. multifasciata*, *S. viridis*, *B. hortensis* and *Isotomurus* spp.) are common particularly in habitats recently disturbed by fire, pollution, defaunation or soil tillage (a sample of such studies is summarised in Table 6.2). These species are also the most common epigeal species found in arable fields. This suggests that arable field species are pre-adapted to the frequent and regular disturbance which is intrinsic to agricultural fields (e.g. spiders, Halley & Lawton 1996). It also suggests that these species are good dispersers since they are able to quickly find and become established in ephemeral habitats. Dunger (1989) suggested that Collembola were amongst the dominant soil microarthropods in early stages of succession.

Despite the apparent ease with which some species colonise ephemeral habitats ('pioneer' species, Table 6.2), mechanisms of dispersal between habitat patches are largely unknown (but see Hertzberg 1997 for an investigation into migration between grass tussocks). Although some Symphypleona could plausibly be dispersed as aerially-transported eggs (Chapter 4), there is no evidence as yet that such a mechanism would also be viable for Arthropleona.

Table 6.2 Examples showing the diversity of habitats in which the common epigeal Collembola of arable fields are also found. a = present study, b = Frampton (1997a), c = Frampton (1994) and references therein, d = Kovac & Miklisova, e = Ehrnsberger *et al.* (1997), f = Cassagnau (1990b) and references therein, g = Vegter *et al.* (1988b), h = Ponge (1993), i = Tamm (1986b), j = Shaw (1997), k = Berg *et al.* (1998), l = Mateos & Selga (1991), m = Mebes & Filser (1997)

Species	Found in the following habitats:					Described as a 'generalist' or 'pioneer' species
	Arable fields	Recently burnt areas	Salt marshes	Open grassland	Woodland	
S. viridis	✓ a,b,c	✓ j	✓ e	✓ d		✓ f
S. elegans	✓ a,b,c			✓ g,h		✓ f
B. hortensis	✓ a	✓ i	✓ e			✓ i
I. viridis	✓ a,b,c,m	✓ i,j	✓ e		✓ k	
I. notabilis	✓ a,b,c		✓ e		✓ k	✓ f
Isotomurus spp.	✓ a,b,c,m	✓ i	✓ e	✓ g,h		
Lepidocyrtus spp.	✓ a,b,c,m	✓ j	✓ e	✓ g,h		✓ f
E. multifasciata	✓ a,b,c	✓ i,j,l		✓ d,g,h		
P. alba	✓ a,c		✓ e			

6.3 The potential of Collembola as bioindicators of non-target pesticide use in arable fields

6.3.1 Biological indicators

Biological indicators are individual species, or species assemblages, which are characteristic of anthropogenic disturbance within defined ecological systems. The need for such indicators arose as a means of monitoring changes, usually detrimental, in an

economically viable, scientifically sound, accurate and descriptive way (Moss 1996). The validity of using particular organisms or groups of organisms as representatives of communities in order to detect environmental change is supported by climax, ecosystem and systems theories (see Kushlan 1993 and references therein). The choice of an indicator species can be made using various criteria. High profile 'flagship' species (Schrader-Frechette & McCoy 1993), which can sometimes be used as 'umbrella' species (see Simberloff 1998 and references therein) have frequently been used in conservation where they can have a strong public appeal. Examples include arabian oryx (Ostrowski *et al.* 1998), lion tamarins (Kleiman *et al.* 1998), and otters and water voles (White *et al.* 1997). However, these species are not chosen to be accurate representatives of change to the ecosystem that they live in. Keystone species (Paine 1969) and 'ecosystem engineers' (Jones *et al.* 1994, 1997) on the other hand have more direct ecological relevance since they comprise species which are considered vital to ecosystem processes. The relative merits of choosing such indicators had been much discussed (see Simberloff 1998 for a recent critique).

Indicators can be chosen from a variety of levels ranging from sub-organismal to ecosystem levels. Their relative advantages are summarised in Table 6.3. The high level of precision and repeatability of sub-organismal measurements (known as 'biomarkers'- see McCarthy & Shugart 1990) are down-weighted by the inaccuracy involved in extrapolating these results to ecosystem-level effects. On the other hand, studying ecosystems is extremely laborious and beset by taxonomic difficulties.

Table 6.3 Ecosystem levels from which biological indicators can be chosen

Level	Sampling units	Advantages	Disadvantages
Individuals:	Organism and suborganism, e.g. tissue samples, behavioural parameters, reproductive potential	•pollutants can be precisely measured •experimental manipulation •direct link to specific stressor •controls can be arranged	•techniques invasive and destructive, may be unethical •extrapolation to ecosystem is difficult •damage by accumulation in food chain may be missed •natural variation between individuals may affect results
Population	species presence / absence, abundance	•can be non- invasive •comparable between similar habitats •fast monitoring methods can be used •specific species monitoring can reduce taxonomic difficulties •experimental manipulation and controls can be set up	•direct link to a stressor can be difficult •experimental manipulation can be difficult, costly or unethical; reliance on monitoring techniques •inter-site differences may not be due to the disturbance being examined
Community or Ecosystem	species presence / absence, diversity indices, abundance	•can be non-invasive •ecosystem level effects detectable •accumulation and interaction effects can be detected	•increasing taxonomic difficulty •time consuming •stressor effects confounded •expensive, potentially unethical to manipulate •difficulty in defining controls

Biological indication with keystone and sensitive species is widely used in monitoring pollution in freshwater ecosystems (e.g. Metcalfe 1989, Moss 1996). There are a growing number of studies that have used a variety of methods to detect community changes and relate them to specific environmental variables. Ruf (1998) showed that an index based on species phenologies of mites could be used to indicate environmental disturbance, whilst bioindicator indices have been developed for toxicant residues and soil pH (van Straalen 1998 and references therein).

The choice of biological indicators for terrestrial systems is at present limited. A number of organisms have been proposed as indicators including: protozoa in field studies (Aescht 1995, Pankhurst *et al.* 1995, Foissner 1997); nematodes to detect disturbance in agroecosystems (Anas *et al.* 1995); heterotrophic flagellates in soil (Ekelund & Christensen 1995); microbial activity in organic fields (Elmholt 1996); protists as indicators of sewage pollution (Warren 1995); butterflies as biodiversity indicators (Kremen 1992); spiders as indicators of non-target pesticide effects (Everts *et al.* 1989); and colonial waterbirds as indicators of environmental change (Kushlan 1993). Several authors have suggested that invertebrates in general are sensitive and accurate indicators of environmental state (e.g. see Siepel & van de Bund 1988, Siepel *et al.* 1989, Kremen *et al.* 1993). Paoletti & Bressan (1996) reviewed the literature on the use of soil invertebrates for monitoring anthropogenic effects and recommended that a great deal more basic research was needed before soil invertebrates could be confidently used as indicators. Van Straalen (1997, 1998) also reviewed soil bioindication systems and concluded that single species indicators were often too variable to be useful and hence an approach based on species composition weighted by ecological attributes was more likely to be effective. Van de Berg *et al.* (1998) also argued for a multi-species approach using food webs.

A strong criticism of the current state of biological indicators in terrestrial ecosystems is that the organisms chosen are frequently arbitrary and their parameters as indicators ill-defined. The use of terrestrial insects as bioindicators requires the functions of a bioindicator system to be defined *a priori*, the organisms chosen and tested accordingly, and differentiation should be carried out between environmental, ecological, and biodiversity indicators (see McGeoch 1998, McGeoch & Chown 1998). Environmental indicators are used to detect and monitor changes in an environmental state. Ecological indicators are used to monitor the impact of a stressor on a biota set and thereby should be representative of the response of the community to this stressor. Biodiversity indicators should reflect species diversity in a specified area and therefore again comprise species representative of a community.

6.3.3 The potential of Collembola as biological indicators

The criteria which have been suggested for choosing a bioindicator, with particular reference to ecotoxicological situations, are summarised on Table 6.4 (see Stork & Eggleton 1992, Barrett *et al.* 1994, McGeoch 1998, van Straalen 1998 for general reviews).

Collembola are numerous and widespread, and may be keystone species, or 'allogenic engineers' (Jones *et al.* 1994, 1997, Lawton 1994) due to their involvement in decomposition and soil nutrient dynamics (e.g. Petersen & Luxton 1982, Kiss & Jager 1987, Mebes & Filser 1998) and as prey items (Bauer 1979, Bauer 1985, Hintzpeter & Bauer 1986, Bauer & Pfeiffer 1991, Kennedy 1994, Sunderland *et al.* 1997). Hence changes to their populations could be indicative of changes in soil 'health' (see Pankhurst *et al.* 1995). They have therefore attracted attention as potential bioindicators of anthropogenic disturbance.

Table 6.4 Criteria for choosing an ecological indicator (amalgamated from Stork & Eggleton 1992, Barrett *et al.* 1994, McGeoch 1998, van Straalen 1998).

Criteria:
I. Species should be numerous in the field to allow valid, ideally parametric, statistically sound comparisons.
II. Species should be geographically widespread so that a bioindicator system can be of general use.
III. Individuals of the species monitored should be expendable if sampling is destructive.
IV. Species should be amenable to manipulation in the field and the laboratory.
V. Species should be easy to sample and convenient to monitor.
VI. Species should be easily recognisable with minimum training and taxonomic difficulties should be minimised.
VII. Sample processing should be time- and cost-effective.
VIII. Researchers should be able to distinguish between pesticide and other agricultural sources of damage to soil communities.
IX. Keystone species with a vital role in the community should be chosen to realistically represent detrimental changes to the ecosystem.
X. Species should be non-target species.
XI. Species sensitive to pesticides should be chosen to provide a worst-case scenario. The sensitivity with which an indicator reacts to change is termed 'resolution' by van Straalen (1998).
XII. It has been suggested that relatively sessile organisms with low immigration rates are useful for monitoring on-site effects (Jones & Kaly 1996).
XIII. Presence and abundance should be to some extent predictable over spatial and temporal scales for monitoring to occur at times when the species is known and therefore expected to be present.
XIV. The stressor effect should be detectable independently of absolute sample size.
XV. Species should demonstrate a well-defined response to the stressor in terms of presence or absence or change in abundance. How specifically an indicator reacts was termed 'specificity' by van Straalen (1998).
XVI. Ecological indicator species should be representative of a change caused by a defined stressor to the community.

Collembola have been proposed as indicators in terrestrial ecosystems of soil acidity (Kopeszki 1992a, van Straalen & Verhoef 1997), indicators of soil physical and chemical properties (Chagnon *et al.* 1996, Kopeszki 1997), and of sulphur dioxide deposition in woodlands (Bressan & Paoletti 1997). In arable ecosystems Collembola have been proposed as indicators of: soil disturbance by tillage and compaction (Heisler 1991, 1993, 1994b, Heisler & Kaiser 1993, Friebe 1993); different soil types (Dunger 1982); heavy metal pollution (Filser 1995b, Filser *et al* 1995, Paoletti *et al.* 1988, 1995); and of non-target effects of pesticides (e.g. Prasse 1985, Joy & Chakravorty 1991, Filser *et al.* 1995, Frampton 1994, 1997a, 1997b).

The suitability of Collembola as ecological indicators of pesticide non-target effects can be evaluated according to the criteria set out in Table 6.2. Requirements I to V are fulfilled by Collembola in arable fields. Certain species are widespread and abundant in arable fields (see studies by Frampton 1988, Filser 1995b, Alvarez *et al.* 1997 *inter alia*). The number of individuals of each species taken in a destructive sample are likely to be expendable (between 10-1000 individuals are caught in a sample covering an area of 0.454 m^2 whilst typical collembolan abundance in a field may be 95 000 per square metre-Diekrugger & Röske 1995). Some species can be cultured and handled in the laboratory (e.g. Wiles & Krogh 1998). Epigeal species can also be conveniently and reliably collected using suction sampling (see section 2.3.2 for sampling considerations).

However, for points VI and VII epigeal Collembola in arable fields are a taxonomically difficult group which require high levels of effort and time dedicated to identification and counting, which presents a serious practical problem to the use of Collembola as indicator species. Taxonomic confusion is likely because of the continuing debate upon the taxonomic status even of common species such as the *Isotomurus* spp. group (e.g. Carapelli *et al.* 1995, Frati *et al.* 1995). Synonymy is prevalent, and there are differences

in opinion among taxonomists as to the degree of morphological difference which can be used to separate species (for a general discussion see Hopkin 1997a, 1997b). The use of morphospecies or functional groups for monitoring could save substantial amounts of time and make collembolan groups a more viable option for monitoring studies. However further work is needed to ascertain the group compositions which would be useful (see Beattie & Oliver 1994, Oliver & Beattie 1996a, 1996b for a discussion on the use of morphospecies for bioindication).

For point VIII, researchers should be able to differentiate between pesticide and other agricultural sources of damage to soil communities. The ability to do this will depend largely on the experimental design, rather than the inherent properties of the bioindicators *per se.* The potential exists for indirect dietary effects of fungicides or of herbicides on refuge plants or organic matter supply to be missed if testing is not conducted under field conditions (sections 1.5, 1.6). Collembola can be considered as viable indicators under the criteria IX to XII. They are ecologically important as prey and detritivores. In Europe they are not generally considered as pest organisms (except for *S. viridis* which is a recognised pest in Spain - Gimeno & Perdiguer 1995, and some Onychiuridae which sporadically attack beet crops - e.g. Hurej *et al.* 1992). Previous studies have shown that in general Collembola abundance is decreased by pesticide use (e.g. Reddersen 1995) and many species are highly sensitive to pesticides (e.g. Wiles & Frampton 1996, Frampton 1988, Frampton 1997b). With regard to point XII, their dispersal rates are poorly known and require further investigation. Whilst some Collembola are considered to be poorly dispersive (e.g. see Cassagnau 1990a) this is not certain and more information is required (see section 4.5).

Collembola were found to be very variable in abundance at different spatial scales (point XIII, see Chapter 5); previous studies have also shown high temporal variations in abundance, with populations sometimes differing by a factor of 50 between consecutive years

(Reddersen 1997). No consistent effect of farming system was detected upon individual species or species groups (point XIV, Chapter 5), nor were any species found which showed a well-defined response and could hence be representative of the communities under different farming regimes (points XV and XVI, Chapter 5). However, in this particular study (Chapter 5) farming regime effectively represented different combinations of stressors (tillage, pesticide use) which were not investigated in isolation. Pankhurst *et al.* (1995) also found that Collembola showed inconsistent responses to tillage management practices and were therefore not potentially useful with respect to criterion XV.

6.3.4 Conclusions

I found that several species of Collembola were ubiquitous in occurrence in cereal and vining pea arable fields, but their populations were spatially variable. The temporal predictability of collembolan species requires further investigation, although previous work suggests a high variability (e.g. see Bengtsson 1994, Filser & Fromm 1995, Moreby *et al.* 1994, Reddersen 1997, Sabatini *et al.* 1997). Wolters (1998) reported year to year fluctuations in collembolan abundance for the same month ranging from 7,600 m^{-2} to 74,900 m^{-2}. My study agrees with most of the existing literature that farming regime is not a major determinant of arable epigeal collembolan populations. Overall the pattern emerging is one of high variability at local spatial scales. Within-field variability is well known in the literature but the importance of variation at a landscape level between fields has been studied less. This is not a good scenario for using Collembola as ecological indicators to monitor pesticide effects since natural population fluctuations would obscure all but very major effects of pesticides. Filser & Fromm (1995), Kovac & Miklisova (1997) and Frampton (1997b) also

encountered the high variation in collembolan populations between fields, although effects of broad-spectrum insecticides on some species were still detected (Frampton 1999).

A lack of differences between farming systems was also found by Reddersen (1997) on a larger scale (all over Denmark). Moreby *et al.* (1994) did find a difference when looking within much smaller regional scales (they investigated eight farms located within the adjacent counties Wiltshire, Berkshire and Oxford in southern England) although results were temporally inconsistent. The high variability in abundance, the difficulties presented by taxonomic uncertainty and the cost associated with labour-intensive identification efforts combine to suggest that Collembola are not ideal for ecological monitoring purposes. Further work is required to investigate whether the direct effects of individual pesticides upon potentially vulnerable species can be detected more widely than in the single fields often used in ecotoxicological studies.

Multivariate techniques including ordination of environmental parameters in conjunction with species abundance data and pesticide use could be used to identify potentially subtle factor combinations of factors involved in determining abundance patterns in the field. The use of field-collected Collembola as test organisms in laboratory and semi-field situations (e.g. Wiles & Frampton 1996) may permit multi-species toxicity testing which is currently limited by the small number of standard test species available. For those Collembola which fulfil the requirements of standard ecotoxicological test organisms (see Wiles & Krogh 1998 for a recent evaluation of *I. viridis, F. candida* and *F. fimetaria* as test species), sensitivity, ecological relevance, and ease of manipulation makes them highly suitable for testing pesticide effects in manipulated situations where the high variation in abundance can be controlled.

6.4 Limitations of the present study

6.4.1 Taxonomic considerations

Rusek (1995) discussed the current state of collembolan taxonomy in relation to ecological studies. He emphasised the state of transition in collembolan taxonomy by pointing out that in 1900 only 118 species of Collembola were known in Europe. By 1960 this figure had risen to 857, and by 1995 2,700 species had been described. Problems occur in synonymy of species, and in the validity of using certain distinguishing features such as setae that may vary between ecomorphs. Information on the biology and behaviour of most species is frequently unavailable and hence the degree of genuine reproductive isolation between potential species is not known. Recent developments using molecular techniques may help to confirm where species barriers occur (Frati *et al.* 1992, 1995, 1999). Few taxonomic keys are available, most of which have become quickly out of date.

Identification also relies upon features which are often not visible except under high magnification. Clearly this imposes limitations upon ecological studies where the volume of individuals can be in the region of thousands per sample and there are limitations to the resources which can be dedicated solely to identification. The use of morphospecies (discussed in Cassagnau 1977, Christiansen & Culver 1968, 1969) for ecological and biodiversity monitoring has been controversially proposed by Oliver & Beattie (Beattie & Oliver 1994, Oliver & Beattie 1993, 1996a, 1996b, 1997; but see Goldstein 1997 for a critique). Hopkin (1997a, 1997b) recommended the use of 'operational taxonomic units' (OTU's) to describe morphologically similar species which may or may not constitute single biological species. At present there is an urgent need for a working key for British Collembola which would enable these organisms to be more readily monitored in ecological

studies. Since springtails appear to be sensitive to a wide range of stressors (e.g. heavy metals, pH, pesticides), it is unfortunate that few ecological investigations take Collembola into account probably because of the taxonomic difficulties associated with them. This study, in common with the majority of ecological studies investigating Collembola, has been limited by the amount of time necessarily devoted to identification difficulties.

6.4.2 Sampling considerations

As previously discussed, Collembola are variable in abundance both spatially and temporally. Increasing the sampling effort could help to reduce variability in the data set and thereby improve the accuracy of the estimated abundance. However, in the present work the number of samples and replication could not be increased mainly due to restrictions on the time available to process samples and identify the collembolan catch. Replication among fields was often also limited by the availability of fields with similar cropping and physical characteristics.

I used suction sampling throughout the investigations presented here. This technique for sampling is limited to dry weather conditions and thus I was unable to monitor collembolan populations in wet conditions. This method may not yield the same species composition of the catch obtained with other sampling techniques (e.g. pitfall traps which can capture nocturnal species, or soil samples which capture edaphic species); but it was considered to provide the best technique for estimating epigeal species abundance. The sensitivity of Collembola to humidity could have biased the catch towards xeric species, although this should not have undermined the validity of the work presented here in which the sampling technique was comparable for all treatment comparisons made.

6.4.3 Farming systems and comparable pesticide treatments

The farming systems employed in this work represented commercial farming practices and as such could not be manipulated. A manipulative approach could have yielded more information on individual components of farming system (e.g. tillage, cropping, pesticide use) but would invariably have compromised agricultural realism.

6.5 Suggestions for further work

Little is known about the population dynamics and long-term survival of fragmented populations of Collembola in arable landscapes. The spatial scales determining collembolan recovery could be investigated in the context of metapopulation dynamics (Hanski 1991, 1994). Such an investigation could help elucidate the mechanisms involved in recovery in fields following pesticide or mechanical perturbations to populations. Long-term studies are also required to determine the factors that govern population size, stability and persistence. Investigation of the regulatory mechanisms for population abundance, specifically whether 'top-down' regulation occurs by beneficial predators, compared to 'bottom-up' resource limitations of field populations (Bonsall *et al.* 1998) is also warranted. This information would be useful for predicting and interpreting indirect pesticide effects upon collembolan populations depending on whether predation or food availability are altered, and to identify whether Collembola can be considered as 'ecosystem engineers' in arable fields. Further work could also help to clarify the role of Collembola as alternative prey items for beneficial arthropods in arable fields, in particular to establish whether springtails distract predators

from target prey species or whether they can help to bolster predator populations during periods when pests are rare.

The lack of definition in the taxonomy of Collembola presents basic problems to the research of their ecology. Many studies have either grouped all the individuals together as Collembola (e.g. Moreby *et al.* 1994), or have classified them only to the family level. It is however imperative that a good working taxonomic order is established in order to study the ecology and importance of particular species in the field.

With regard to the effects of dry conditions upon collembolan eggs, it still remains to be tested whether this life stage is important for collembolan dispersal, particularly among Arthropleona which appear to have less tolerant eggs than Symphypleona. The dispersal mechanisms used by Collembola over landscape scales and between different habitats represents an important gap in the knowledge of the basic ecology of this group.

Appendices

Appendix I. The effects of other pesticides used in arable fields upon Collembola in field and laboratory studies.

*References in Edwards & Thompson (1973). n/a = not applicable; n.a. = information not available

Pesticide:	Lab or Field	Collembola species / taxa	Crop	Effects	Author
Aldicarb- carbamate insecticide and nematicide	Lab	*Folsomia candida*	n/a	Negative effects.	Thompson & Gore (1972)
Bacillus thuringiensis - bacterial insecticide	Lab	Collembola	n/a	In a 45-day lab. Experiment found that Collembola decreased by 2 to 10 times.	Addison (1993)
Bacillus thuringiensis	Field	Collembola	Not specified	Over 45 days found Collembola (and Acarina) decreased by 2-10 times.	Atlavinyte *et al.* (1982)
Bacillus thuringiensis	Field	*F. candida*	Transgenic cotton and potato	No effect upon oviposition, egg production or final body length when fed BT in transgenic leaves and tubers.	Yu *et al.* (1997)
Methyl-bromide - nematicide and sometimes used as an insecticide.	Lab	Collembola	n/a	Negative effects.	Edwards, Reichle & Crossley (1969)*
Methomyl - carbamoyloxine insecticide for fly control in animal houses.	Lab	*F. candida*	n/a	Negative effects.	Edwards & Lofty (1971)*, Thompson & Gore (1972)
Methomyl	Lab and field	Collembola general	Hops	Laboratory and field studies often contradictory about lethal and sublethal effects even within species.	Filser & Nagel (1993)

Appendix I continued...

Pesticide:	Lab or Field	Collembola species / taxa	Crop	Effects	Author
Methiocarb - a carbamate molluscicide and insecticide	Lab and field	Collembola	n.a.	Generally toxic.	Eddy (1969)
Methiocarb	Field	Collembola amongst arthropod fauna	Winter wheat	No significant effect.	Kelly & Curry (1985)
Methiocarb	Semi-field	Collembola	n.a.	No significant effect.	Kennedy (1988)
Methiocarb	Field	Collembola including *Sminthurus viridis*	Arable field	More Collembola in direct-drilled fields, community dominated numerically by *S. viridis* after burning.	Martin (1993)

Appendix II. The effects of fungicides upon Collembola in recent field and laboratory studies.

*References in Edwards & Thompson (1973). n/a = not applicable; n.a. = information not available

Fungicide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Aktuan - systemic organic fungicide containing cymoxanil and dithianon	Field	*Proisotoma minuta, Hypogastrura assimilis, I. Palustris, Entomobryidae, I. notabilis, Neelus minimus, L. cyaneus & L. lanuginosus*	Hops	Negative but potentially statistically flawed.	Filser (1994)
Benomyl	Lab	Collembola	n/a	Generally toxic although effects vary between species; no long term effects.	Krogh (1991)
Benomyl	Lab & field	Collembola	n/a	Insecticidal effects but not long-term.	van Straalen & Rijn (1998)
Carbendazim (breakdown product of Benomyl)	Field	*Sminthurus viridis*	Wheat plots	Negative - lethal.	Frampton (1989)
Carbendazim	Lab	*Sminthurinus aureus*	n/a	Negative - lethal.	Frampton (1989)
Carbendazim	Lab	*Isotoma viridis*	n/a	Negative - lethal.	Frampton (1989)
Carbendazim	Field	*Isotoma viridis*	Winter wheat	Negative - decreased field abundance.	Frampton (1989)
Chlorpicrin	Field	Collembola	Wood stumps	Negative effect: significantly reduced populations.	Moldenke & Thies (1996a)

Appendix II continued...

Fungicide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Fenarimol	Lab	*Folsomia candida*	n/a	Negative- high toxicity to Collembola.	Kiss & Bakonyi (1990)
Metalaxyl- phenylamide fungicide	Field	Collembola	Vines	Negative- residual effect.	Kaluz *et al.* (1993)
Pentachloro-phenate	Lab	*Folsomia candida*	n/a	Negative.	Gruttke *et al.* (1988)
Propiconazole	Lab	*Isotoma viridis*	n/a	Not toxic; sublethal effects not quantified.	Frampton (1989)
Propiconazole	Lab	*Sminthurinus aureus*	n/a	Significant negative effects.	Frampton (1989)
Propiconazole	Field	*Isotoma viridis*	Winter wheat	Negative: reduced population levels.	Frampton (1989)
Propiconazole	Lab	*Folsomia candida*	n/a	Negative- slightly less toxic than Fenarimol.	Kiss & Bakonyi (1990)
Propiconazole	Field	*Sminthurus viridis*	Wheat plots	Negative: adverse effects, lethal.	Frampton (1989)
Pyrazophos	Field	Collembola	Winter barley	Duration of effect varied with plot size.	Sotherton *et al.* (1987)
Pyrazophos	Lab	*Isotoma viridis*	n/a	Not directly toxic but may have sublethal effects.	Frampton (1989)
Pyrazophos	Lab	*Sminthurinus aureus*	n/a	Negative: lethal very quickly.	Frampton (1989)

Appendix II continued...

Fungicide:	Laboratory or field study	Collembola species	Crop	Effects	Author
Pyrazophos	Field	*Sminthurinus aureus, S. elegans, Sminthurus viridis, J. stachi,* total Arthropleona, total Symphypleona	Winter barley	Took longer to act than dimethoate, and recovery took a longer time.	Frampton (1989)
Sulphur - fungicide	Field	Collembola	Hops	Detrimental.	Filser (1993)
Triadimenol	Lab	*Isotoma viridis*	n/a	Not toxic - possibly sublethal effects.	Frampton (1989)
Triadimenol	Field	*Isotoma viridis*	Winter wheat	Negative: harmed population levels.	Frampton (1989)
Triadimenol	Lab	*Sminthurinus aureus*	n/a	Negative- lethal.	Frampton (1989)
Triadimenol	Field	*Sminthurus viridis*	Wheat plots	Negative: adverse effects, lethal.	Frampton (1989)

Appendix III. Effects of herbicides upon Collembola in field and laboratory studies.

*References in Edwards & Thompson (1973). n/a = not applicable; n.a. = information not available

Herbicide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Atrazine	Field	Hemiedaphic Collembola	Meadow	Negative: decreased abundance.	Fox (1964)
Atrazine	Field	Collembola	Corn	Negative: significantly reduced populations.	Popovici *et al.* (1977)
Atrazine	Lab	*F. candida, Tullbergia granulata*	n/a	Fed in food (yeast); lethal.	Subagja & Snider (1981)
Atrazine	Field	Collembola	Corn	Positive: increased populations probably by increased soil litter. May have a sublethal effect?	Moore *et al.* (1984)
Atrazine	field	Collembola	Corn	Positive: enhanced populations.	Mallow *et al.* (1985)
Atrazine	Field	Collembola	Maize	Negative.	Fratello *et al.* (1985, 1986)
Atrazine	Field	Hemiedaphic Collembola	Meadow	Positive: enhanced populations, probably due to increased litter.	Conrady (1986)
Atrazine	Lab	*Onychiurus apuanicus and O. armatus*	n/a	Negative: lethal. Mortality especially high on sand substrate.	Mola *et al.* (1987)
Atrazine	Lab	*Orchesella cincta*	n/a	Negative on growth and reproduction.	Badejo & van Straalen (1992)

Appendix III continued...

Herbicide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Atrazine	Field	Collembola	Maize	No significant differences due to atrazine applications, rather to the mulching.	Wardle *et al.* (1993)
Atrazine	Field and lab	*Entomobrya musatica*	Cotton and maize since 1980; but current crop not specified	Field: negative, overall population decreased. Lab: at low levels no observed effect; at high levels slower development, higher mortality and lowered fecundity.	Al-Assiuty & Khalil (1996)
Atrazine	Field and lab	Collembola	n/a	Detrimental and no observed effect in lab. Long term detrimental effects in the field.	van Straalen & van Rijn (1998)
Bromacil	Field	Collembola	Maize	No significant differences.	Wardle *et al.* (1993)
Caragard	Field	Collembola	Maize	No significant differences.	Wardle *et al.* (1993)
Cyanazine	Field	Collembola	Cereals	Negative: reduced populations.	Edwards & Stafford (1979)
Dalapon and TCA	Field	Collembola	Meadow	Positive- increased abundance.	Fox (1964)
2,4-D	Field	Collembola	Meadow	Little or no effect.	Fox (1964)

Appendix III continued...

Herbicide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Fluazifop.	Lab	*Folsomia candida*	n/a	Negative: slight on direct exposure, also sublethal effects.	Kiss & Bakonyi (1990)
Hexazinone	Field	Collembola	n/a	Negative effects.	Badejo & Adejuyigbe (1994)
MCPB	Field	Collembola	Maize	No significant differences due to applications; increases due to mulching.	Wardle *et al.* (1993)
P-nitrophenol	Lab	Collembola	n/a	Negative effects.	Parmelee *et al.* (1993)
Paraquat	Lab	*F. candida*	n/a	Fed in food; not lethal.	Curry (1970)*
Paraquat-	Lab	*Folsomia candida, Tullbergia granulata*	n/a	Sublethal and lethal effects were noted.	Subagja & Snider (1981)
Paraquat-	Field	Collembola	n.a.	Negative or no observed effect.	Fratello *et al.* (1986)
Paraquat-	Field	*I. notabilis*	n.a.	Positive- increased density.	Curry (1970)*
Rimsulfuron	Field	Collembola	Maize	No significant differences.	Wardle *et al.* (1993)
Simazine	Field	Collembola	Cereal	Negative: abundance reduced by 70%.	Edwards (1970)*
2,4,5-T - 2,4,5-trichlorophenoxyacetic acid	Lab	*Onychiurus quadriocelatus (Protaphorura quadriocellata)*	n/a	Negative: both direct toxicity and behavioural (avoidance) effects.	Eijsackers (1975), Fratello *et al.* (1986)
2,4,5-T	Lab	*Onychiurus quadriocelatus (Protaphorura quadriocellata)*	n/a	Negative: directly toxic, also sublethal effects: avoidance and locomotion affected.	Eijsackers 1978

Appendix IV. The effects of insecticides upon Collembola in field and laboratory studies.

*References in Edwards & Thompson (1973). n/a = not applicable; n.a. = information not available

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Aldicarb	Field	Collembola	Grass swards	Toxic short term but recovery within 10 weeks.	Ellis *et al.* (1990)
Aldicarb, aldicarb-sulfone	Lab- microcosms	Collembola	n/a	Toxic- though Collembola less affected than Acari; the derivative is less toxic.	Born *et al.* (1989)
Aldrin	Field	*Protaphorura hortensis*	Bean field	Negative.	Edwards (1962)*
Aldrin	Field	Collembola	Arable field	Short-term negative effects but quick recovery.	Edwards *et al.* (1967)
Aldrin	Field	Collembola	n.a.	Reduced population levels persistently.	Joy & Chakravorty (1991)
Aldrin	Field	Collembola	Arable field	Negative effects- though some recovery over time.	Edwards & Dennis (1960)*, Fox (1967)
Aldrin	Lab	*F. candida*	n/a	Bioassays showed positive or no effect.	Griffiths *et al.* (1967)
Aldrin	Lab	*F. candida*	n/a	Least toxic out of carbaryl, parathion, lindane, diazinon.	Thompson & Gore (1972)
BHC -organochlorine	Field	Collembola	n.a.	Negative effects.	Hitcock (1953)*, Cramer (1956)*, Sheals (1955)
BHC -organochlorine	Field	Collembola	n.a.	Positive effects.	Richter (1953), Dobson & Lofty (1956)*, Bauer (1964)*, Wallace (1959)

Appendix IV continued...

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Carbamates and various organophosphates	Field	*Onychiurus pseudarmatus*	n.a.	Both highly toxic, used for control of pest Collembola.	Getzin (1985)
Carbofuran	Lab and field	*Folsomia candida*	Winter oil seed rape	Negative.	Achick (1989)
Carbofuran	Lab and field	Collembola from soil cores	Pasture	Negative.	Martin (1976), (1978)
Carbosulfan	Lab and field	*Folsomia candida*	Winter oil seed rape	Negative: least toxic of 4 studied.	Achick (1989)
Chlordane	Field and lab	Collembola	Agricultural soils	Detrimental effects in both field and lab.	Joy & Chakravorty (1991)
Chlordane	Field	Collembola	n.a.	Negative effects which affected population levels for several years.	Edwards (1977), Thompson & Gore (1972)
Chlorfenvinphos-	Field	Collembola	n/a	Positive: resurgence of population.	Edwards & Thompson (1973)
Chlorpyrifos	Lab	*F. candida* - 4 different clones	n/a	All strains were similarly negatively affected.	Crommentuijn *et al.* (1995)
Chlorpyrifos	Lab- on field soil	*S. viridis, F. candida, I. palustris, I. viridis*	Soil sprayed under a cereal crop	Negative; residues were especially toxic where no cereal plant cover was present.	Wiles & Frampton (1996)

Appendix IV continued...

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Cypermethrin	Field and lab	*S. viridis, F. candida, Isotomurus palustris, Isotoma viridis*	Soil sprayed under a cereal crop	Negative; residues were especially toxic where no cereal plant cover was available.	Wiles & Frampton (1996)
Diazinon	Field	Collembola	Arable field	Positive.	Edwards *et al.* (1967)
DDT	Field	Collembola	n.a.	Positive: resurgence of population.	Wallace (1954)
DDT	Field	Collembola	n.a.	Positive: resurgence of population.	Sheals (1955)
DDT	Field	Collembola	n.a.	Positive: resurgence of population.	Edwards *et al.* (1967)
DDT	Field	Collembola	Forest floor	Positive: resurgence of population.	Knight & Chesson (1966)
DDT	Field	Collembola	Grass-land	Positive: resurgence of population.	Fox (1967)
DDT	Lab	*F. candida*	n/a	DDT converted to DDE by the Collembola.	Butcher *et al.* (1969)
DDT	Field	Collembola	n.a.	DDT accumulated in tissues.	Lupetti *et al.* (1994)
DDT	Field	Collembola	Forest soil	Negative.	Perfect *et al.* (1981)
Dieldrin	Field	Collembola	n.a.	Negative.	Davis (1966)
Dieldrin	Lab	*F. candida*	Arable field soil	Negative.	Thompson (1973)
Diazinon	Field	Collembola	n/a	Positive: resurgence of population.	Edwards *et al.* (1967)
Diazinon	Lab	*F. candida*	n/a	Negative: direct toxicity lethal.	Kiss & Bakonyi (1990)

Appendix IV continued...

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Disulfoton	Lab	*F. candida*	n/a	Negative effects: toxic.	Thomson & Gore (1972)
Dimethoate	Field	*S. viridis, S. aureus, J. stachi, S. elegans*, total Symphypleona	Winter barley	Negative: strong population reductions short-term.	Frampton (1989)
Dimethoate	Lab	*Folsomia fimetaria*	n/a	Negative: body growth shown to be a good parameter for dimethoate effect, sex and species-specific.	Folker-Hansen *et al.* (1996)
Dimethoate	Lab	*F. candida*	n/a	On different soil types: Collembola more susceptible than enchytraeid worms.	Martikainen (1996)
Dimethoate	Lab	*F. candida*	n/a	Negative: sublethal effects affecting locomotion even at low concentrations.	Sørensen *et al.* (1995)
Dimethoate	Field	*S. viridis* among other Collembola	Winter barley	Negative: reduced population levels.	Frampton (1988)
Endosulfan	Field	Collembolan abundance and biomass	Hops	Negative; but increased abundance in 1 field due to green manure; but note the lack of replication (2 fields).	Filser (1990)
Endosulfan	Lab	Collembolan abundance and biomass	Hops	Negative on abundance and biomass.	Filser (1990)
Endosulfan-	Lab	Collembola	n/a	Detrimental.	Fromm & Filser (1991)

Appendix IV continued...

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Endosulfan-	Lab and field	Collembola		Negative.	Joy & Chakravorty (1991)
Fenthion	Field	Collembola	n.a.	Negative effects: toxic.	Wibo (1973)
Fonofos - organophosphorus insecticide soil and seed treatments	Lab	Collembola	n/a	Negative effects with bioassays using field soils: toxic.	Griffiths *et al.* (1967)
Heptachlor	Field	Collembola	Grassland	Negative effects.	Fox (1964), Thompson & Gore (1972)
Isobenzan	Lab	*F. candida*	n/a	Negative effects.	Thompson (1973)
Isobenzan	Field	Collembola	n.a.	Negative effects.	Kelsey & Arlidge (1968)*, Thompson & Gore (1972)
Lindane	Field	*Protaphorura hortensis*	Beans	Negative.	Edwards (1962)
Lindane	Field	Collembola	Sugar beet	Negative.	Czarnecki & Losinski (1985)
Lindane	Field	Collembola	n.a.	Negative.	Gregoire-Wibo (1983)
Menazon	Field	Collembola	n.a.	Negative effects: toxic.	Madge (1981)
'Organochlorine'	Field	Collembola, including *S. viridis*	Grass	Initial toxicity but very rapid recovery (probably due to the insecticide killing off predatory mites).	Wallace (1959)
Collembola	Field	Collembola	n.a.	Positive: resurgence of population.	Wallace (1959), Edwards & Thompson (1973), Baudissin (1952)
Parathion	Field	Collembola	n.a.	Negative.	Richter (1953)

Appendix IV continued...

Insecticide:	Laboratory or field study	Collembola species / taxa	Crop	Effects	Author
Permethrin	Lab	*F. candida*	n/a	Negative: direct toxicity lethal.	Kiss & Bakonyi (1988)
Phorate	Field	Collembola	n.a.	Negative effects: toxic.	Edwards *et al.* (1967), Thomson & Gore (1972), Way & Scopes (1968)
Plyphosphate-	Lab	*F. candida*	n/a	Negative: slight toxicity on direct exposure, also sublethal effects.	Kiss & Bakonyi (1990)
Pirimicarb	Field and lab	*S. viridis, F. candida, Isotomurus palustris, Isotoma viridis*	Soil sprayed under a cereal crop	Negative; residues were especially toxic where no cereal plant cover was available.	Wiles & Frampton (1996)
Tebofenozide	Lab	*F. candida, Hypogastrura panosa, Onychiurus sp., F. nivalis*	n/a	In microcosms. No significant deleterious effect.	Addison (1996)
Terburofos	Lab and field	*F. candida*	Winter oil seed rape	Negative: most toxic of 4 chemicals tested.	Achick (1989)
Thiofanox	Lab and field	*F. candida*	Winter oil seed rape	Negative: second most toxic. In field though this was the least toxic and persistent.	Achick (1989)
Thionazin	Lab and field	Collembola	Wheat	Positive: resurgence of population.	Griffiths *et al.* (1967)
Thionazin	Lab	Collembola	n/a	Positive or no effect: not toxic.	Griffiths *et al.* (1967)
Thionazin	Lab	Collembola	n/a	Negative.	Edwards & Thompson (1973)

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