Linyphiid spider populations in sustainable wheat-clover bi-cropping compared to conventional wheat-growing practice

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Isotoma anglicana, agrobiont spiders, non-crop habitat, path diagram, reproduction

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Abstract

Linyphiid web densities in wheat-clover bi-crop systems where winter wheat was grown in an under-storey of white clover were compared with web densities estimated in conventional wheat-growing systems. The web densities in the wheat-clover bi-crop systems were on average between 200 and 250 webs per square-metre when the densities peaked, while the estimated average web density peak levels under conventional growing practices were 100–150 webs per square-metre. Repeated Measure ANOVA tests show significant differences between the estimated mean web density levels of the bi-crop systems compared to the mean density levels of the conventional growing systems in two consecutive growing seasons. Particularly, *Bathyphantes gracilis* and *Tenuiphantes tenuis* took advantage of the more heterogeneous conditions with high secondary vegetation layer density and high food animal supply in the bi-crop plots compared to the more homogeneous conditions under conventional wheat-growing practices with low food animal supply. Structural equation modelling with a data set pooled from four different wheat-growing practices shows that the linyphiid juvenile production is influenced by the number of collembolans accessible as food animals for the adult females. The modelling demonstrates the importance of the detritus food chain, particularly for the juvenile recruitment.

Introduction

The presence of mulch in cereal crops (Schmidt et al. 2004) as well as the integration of non-crop, perennial habitats in crop fields seem to be optimal choices when the intention is to increase the spider population density in cereal fields (Sunderland and Samu 2000), and Schmidt et al. (2004) showed that enhanced densities of spiders in mulched plots presumably resulted in a 25% reduction in the aphid densities in June, and their results indicate that a scarcity of ground-dwelling predators and bare soil surface renders crops more susceptible to arthropod pests, particularly aphids.

Growing wheat in leguminous living mulch (bi-cropping) such as white clover, therefore, seems to be a promising alternative to conventional wheat-growing practice with ploughing every year, which results in bare soil surfaces between the crop plants during the growing season. In this experiment, winter wheat was grown in a permanent vegetation layer consisting of white clover. The purpose of growing wheat in living mulch such as white clover is to reduce the use of fossil fuel energy for tillage and other agricultural operations as well as reducing the consumption of fertilizers. The goal is to minimize, or completely avoid, the use of pesticides while preventing losses of nutrients and increasing soil biological activity.

This increases the diversity of the sward (Harwood and Obrycki 2005). Alderweireldt (1994) has shown that increasing the diversity of Belgian crop fields increased spider densities. More specifically, *Bathyphantes gracilis* Blackwall 1841 and *Tenuiphantes* *tenuis* Blackwall 1852 (formerly *Lepthyphantes tenuis*) took advantage of habitat manipulation, where the soil surface was made more heterogeneous. Increasing the abundance of under-storey vegetation – particularly clover mulch – seems to increase both density and numbers of linyphiid spider species within different farming systems (Altieri et al. 1985; Feber et al. 1998).

Research using isotope analysis suggests that the detritivores represent a key food resource for linyphiid spiders (McNabb et al. 2001; Wise et al. 2006), and Marcussen et al. (1999) concluded that a high abundance of the Collembola species *Isotoma anglicana* Fjellberg 1980 can support a high reproductive output for *Erigone atra* Blackwall 1841. This puts a focus on the link between collembolans and the detritus food chain in cereal fields. Input of organic material to the soil surface as well as under sown clover grass may increase the densities of collembolans (Axelsen and Kristensen 2000).

This supports the idea that bi-cropping with a permanent, secondary vegetation layer consisting of white clover may enhance the organic matter content in the topsoil, which may have a beneficial impact on the Collembola density at the soil surface. Moreover, enhanced Collembola densities may further support higher reproductive outputs of the agrobiont linyphiid spiders in the cereal fields.

To get a better understanding of the relationships between the different factors involved in the population dynamics of agrobiont linyphiid spiders, the multivariate statistic analysis procedure called structural equation modelling (Arbuckle and Wothke 1999; Shipley 2000) was used in this study for exploratory purposes. Structural equation modelling (SEM) is a powerful statistical technique that is used to estimate, analyse and test models that specify relationships among variables. The view of SEM was first articulated by the geneticist Wright (1921), but the statistical method was largely ignored by the biology community up through the twentieth century (Shipley 2000).

The SEM procedure usually starts with a hypothesis considering the relationships between the involved variables. In this study, exploratory modelling is specified on the basis of theory, which is supported by information from the available literature. Supported by this information, a model is built on the basis of hypothesized relationships among the sampled variables. The relationships between five variables are analysed and a model is tested by using the statistical programme AMOS (Analysis of Moment Structures; Arbuckle and Wothke 1999).

Methods

Site

Field research was carried out at the agricultural Research Centre Foulum (9°34′E, 56°30′N), approximately 10 km east of Viborg, Denmark. The soil type in the experimental area at Research Centre Foulum is a sandy soil with 8% clay. The experimental area was surrounded by areas of permanent white clover (cv. Donna) vegetation, sown simultaneously with the white clover (cv. Donna) in the experimental wheat-clover bi-crop plots. The establishment of the white clover was performed in the spring of 1994. The first winter wheat crop (cv. Hereward) was established in September 1994, the second winter wheat crop in September 1995 and the third winter wheat crop in September 1996.

The winter wheat in the bi-crop plots was directly drilled into a defoliated white clover sward using a combined cultivator and sowing machine (Hunter Rotary Strip Seeder, Hunters Machinery, Tarporley, Cheshire, UK) that drilled 7.5 cm wide slots in the clover sward with a drilling distance of 23 cm between each wheat row. This left some dead plant material and just a short clover layer when the new wheat crop was established. Establishment of the winter wheat crop in the conventionally grown plots was done by sowing the wheat into a conventionally ploughed seedbed with a row distance of 23 cm.

Experimental design

Field research was carried out in May–October 1995 as well as June–September 1996 and in July 1997 in 16 experimental plots (each 12 × 50 m), representing four different growing systems. The experimental plots were located in a randomized complete block design with the four agricultural treatments replicated four times. Web distance measuring to estimate the linyphiid web densities as well as other sampling procedures was done inside a 10 × 10 m quadratic area in the middle of each of the experimental plots.

The four agricultural treatments were either wheat-clover bi-cropping – BU without nitrogen fertilization and BL with nitrogen fertilization (50 kg/ha) – or conventional wheat-growing – CL with low nitrogen (50 kg/ha) and CH with high nitrogen (160 kg/ha) input. The BU, BL and CL plots did not receive any pesticide treatment, whereas the CH plots received 'normal' pesticide treatment that is common in intensively grown Danish winter wheat fields: Bentazon 1200 g active ingredient (AI) per hectare (Basagran

J. Appl. Entomol. **132** (2008) 545–556

480, BASF, Ludwigshafen, Germany) herbicide to control dicotyledons in the spring of 1995, 1996 and 1997; propiconazol 90 g AI/ha + fenpropimorph 210 g AI/ha (Tilt Megaturbo, Syngenta, Basel, Switzerland) fungicide to control fungi in the wheat crop in June 1995, propiconazol 90 g AI/ha + fenpropimorph 260 g AI/ha (Tilt Top, Syngenta, Basel, Switzerland) fungicide to control fungi in the wheat crop in June 1996 and prochloraz 450 g AI/ha (Sportak, BASF, Ludwigshafen, Germany) fungicide to control fungi in the wheat crop in late May 1997; pirimicarb 125 g AI/ha (Pirimor, Syngenta, Basel, Switzerland) insecticide to control aphids in July 1995; and glyphosate 900 g AI/ha (RoundupBio, Monsanto, St Louis, MO, USA) herbicide to control grass weeds before harvest in August in both 1995 and 1996.

Sampling procedure

In our use of the web distance measuring procedure, we followed the sampling procedure given by Toft et al. (1995). A bamboo stick was placed at a random point (sampling point) within the experimental plot. To make the webs more easily observable, the area around the sampling point was sprayed with white talcum powder. The area was then searched for webs, which were marked one by one with thin metal marker sticks. The metal sticks were placed in the centre of each web, and the distances from the sampling point to each of the metal sticks were measured. The distances to 10 web centres were measured, and the web density was estimated on basis of the distance from the sampling point to the fifth closest web (fig. 1a). Consecutive web density estimations were performed in each of the 16 experimental plots. Web density estimations were performed once each month between May and October in 1995, while in 1996 the web density estimations were performed with shorter intervals between June and September. In 1997, the web density estimations were done just once in July.

When the web distance measuring procedure was combined with vegetation density estimation, web distances followed by vegetation height were measured. A ring with a diameter of 40 cm was placed with the sampling point in the middle (fig. 1b), and the vegetation was cut, leaving only 2 cm stubbles (fig. 1c).

Only the lower vegetation layer, which includes the clover and weed layer, was density-estimated on basis of the vegetation layer heights and the vegetation dry weights. The combination of web density estimation and vegetation density estimation was

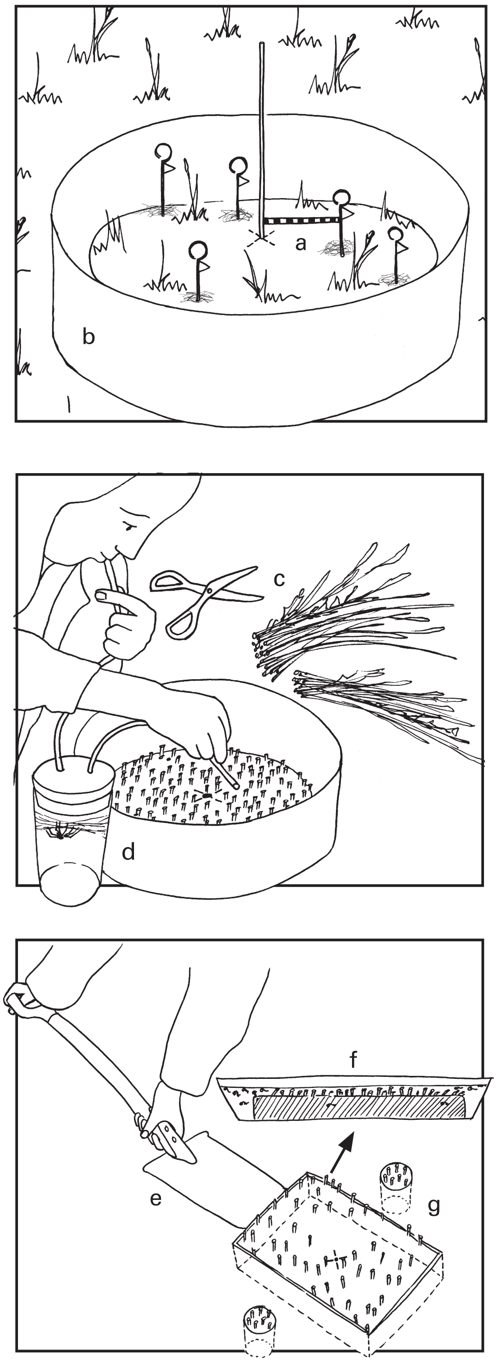

Fig. 1 (a–g) Sampling procedures. See text for further explanation.

performed on six occasions in 1995, nine in 1996 and on one occasion in 1997.

In a more intensive sampling period in the summer of 1996, web distance measuring was combined with both vegetation density estimation and sampling of live linyphiid spiders (fig. 1d). The sampling of live spiders was not only restricted to the plastic ring but was also extended to an enlarged area around the ring. To prevent the spiders from escaping, a plastic barrier was placed around the enlarged area. The vegetation inside the ring was cut and used for the vegetation density estimation. The vegetation in the enlarged area was also cut, and all harvested vegetation as well as bare soil was searched for live spiders, which were sampled with a pooter. The area inside the plastic ring plus the enlarged area around the ring, enclosed by the plastic barrier, had a total area of 0.48 m^2.

In the intensive sampling period, soil surface samples for collembolans as well as soil samples for soil water and organic matter contents were taken on both sides (north–south) of the sampling point. The soil surface sampling for collembolans was done by shovelling the soil surface to a depth of 1 cm inside an iron frame measuring 10×20 cm (fig. 1e), and soil with collembolans was afterwards kept in alcohol (concentration 40%) (fig. 1f). Soil samples for measuring soil water and organic matter content were finally taken with a cylindrical soil sampler (diameter 5 cm) to a depth of 5 cm in the topsoil (fig. 1g).

All the coordinated sampling procedures (in the intensive sampling period) were completed within 1 h at each experimental plot, thereby ensuring consistency for comparative purposes. Sampling was done between 10 am and 4 pm. The sampling in each experimental plot was performed with a new sampling point at least 1.5 m from former sampling points to ensure optimum independence of former samplings. Consecutive samplings in the 16 experimental plots were performed within 1 day – always starting at the northern end of the row of experimental plots and finishing at the southern end of the row. All sampling procedures in the intensive sampling period were performed consecutively through all 16 experimental plots at seven occasions within 8 weeks starting in week 25 in June 1996 and ending in week 32 in August 1996.

Sample Analysis

Webs

The web density estimation requires the webs to have a random dispersion pattern. The dispersion pattern was tested using Eberhardt's index for point-to-nearest web distances: $\mathrm{IE} = (s/\mathrm{avg})^2 + 1$, where s is the standard deviation and avg is the average of the distances from the sampling point to the nearest web (Krebs 1989). The expected value of IE in a random population is 1.27. Values below this suggest a regular pattern, and larger values indicate clumping. See also critical values for Hines Test Statistics hT (Krebs 1989).

On basis of point-to-nearest web distance measurements in a period from May 1995 till September 1996, calculated values of the Eberhardt's index indicate random dispersal of linyphiid webs on 13 out of 14 sampling dates in the bi-crop plots and on 11 out of 14 sampling dates in the conventional plots. The index values were calculated on the basis of pooled data sets for both the bi-crop systems and the conventional systems together. In June 1995, the web dispersal pattern in the bi-crop plots as well as in the conventional plots indicated a clumped dispersal pattern. In the conventional plots, the Eberhardt's index values indicate uniform dispersal on two dates – in August 1995 as well as in July 1996. In general, the assumption of random distribution seems fulfilled, and therefore the density estimation formula can be applied.

The web density is estimated on the basis of a distance method where the distance from a randomly selected point to the nth nearest individual has been measured (Keuls et al. 1963; Southwood and Henderson 2000). As Toft et al. (1995) showed, there is little to be gained by extending the observations past the fifth web. We used the distance to the fifth closest web from the randomly placed sampling point and then estimated the web density by a formula provided by Keuls et al. (1963): the estimate of the density $N_4 = (q\text{-}1)/\pi r q^2$. In this study, $N_4 = 4/\pi r q^2$, when $q = 5$ and r is the distance to the fifth closest web.

Spiders caught alive

All spiders caught alive were kept in individual plastic containers for 1 week, each with a code number used to identify the adult spiders as to species. If the spiders produced cocoons, the containers were kept until juveniles hatched. The juveniles were counted, and on basis of this procedure it was possible to estimate the absolute juvenile production per squaremetre on the basis of the counts and the area of the enclosure where the adults were caught (Sunderland and Topping 1995).

During the intensive sampling period in the summer of 1996, the total linyphiid juvenile production was estimated for each sampling occasion, and the values were used in the multivariate statistic analysis and data sets of total numbers of adult spiders caught in each of the 16 experimental plots were

J. Appl. Entomol. **132** (2008) 545–556

constructed for *B. gracilis* and *T. tenuis*, and were used in the variance analysis in relation to the four different agricultural practices.

Vegetation

The secondary vegetation layer, consisting of clover and weed plants, was density-estimated on the basis of the height of the secondary vegetation layer and the vegetation dry weight. The dry vegetation was weighed after it was dried out to a constant weight in an oven for at least 24 h.

The secondary vegetation layer densities were estimated on the basis of sampling done at seven dates during the intensive sampling period in the summer of 1996. On basis of the samplings in each of the 16 experimental plots, the average secondary vegetation layer density for each plot was calculated. The data set with the 16 average values of secondary vegetation layer densities was used to compare the mean secondary vegetation layer densities in relation to the four different growing practices.

The total lower vegetation layer density was estimated on the basis of the secondary vegetation layer density plus the wheat crop density. The wheat crop was density-estimated on the basis of that part of the wheat plants present in the secondary vegetation layer. The wheat crop density was estimated in a similar way as the secondary vegetation layer density. The total lower vegetation layer density estimations were used in the correlation test as well as in the multivariate statistic analysis.

Collembola

Collembolans in soil samples with alcohol were separated from the soil using glycerine to drive out the animals from soil pores, and the collembolans were roughly identified and counted. On the basis of the sampling procedure using an iron frame with an area of 200 cm^2, it was possible to estimate the Collembola density in the soil surface.

The Collembola densities in the soil surface were estimated on the basis of sampling done at seven dates during the intensive sampling period in the summer of 1996. On the basis of the samplings in each of the 16 experimental plots, the average Collembola density during the intensive sampling period was calculated for each plot. The data set with the 16 mean values of Collembola densities were used to compare the mean Collembola densities in relation to the four different growing practices, and the estimated Collembola density values of each sampling occasion were used in the multivariate statistic analysis.

Soil

The soil water content was calculated by first measuring the fresh weight of the soil samples, after which the soil samples were dried out to a constant weight at 105°C for 2–3 days. On the basis of the difference between the fresh weight and the dry weight divided by the fresh weight, it was possible to calculate the percentage content of soil water in the upper 5 cm of the topsoil (Schierup and Jensen 1981).

Soil samples dried out to a constant weight were burned in an oven at 550–600°C for 6–8 h. The percentage content of organic matter in the topsoil was then calculated in a similar way as with the soil water content by calculating the dry weight of the soil samples minus the burned weight divided by the dry weight. Calculated organic matter and soil water content were used to compare mean organic matter as well as mean soil water content in relation to the different growing practices. The calculated organic matter and soil water content values of each sampling occasion were also used in the multivariate statistic analysis.

Arthropod identification

Spiders were identified in agreement with Roberts (1987), and collembolans were identified in agreement with Fjellberg (1980).

Statistical Analysis

Transformations

On the basis of normality tests with raw variables, the estimated vegetation densities used in the correlation test as well as the numbers of adult linyphiid spiders used in the variance test were left as untransformed data sets while other data sets were transformed before the statistical analysis. The estimated web densities, numbers of Collembola in the soil surface and numbers of produced juveniles were log-transformed. The percentages of soil water and organic matter content were arcsine-transformed, and the estimated vegetation densities used in the multivariate statistic analysis were transformed as reciprocal transformations. The results of these transformations are data sets approximately normally distributed and with equal variances between treatments.

Finally, the multivariate data set used in the SEM was evaluated using a multivariate normality test, which shows a multivariate kurtosis value of 1.58 (Mardia's coefficient). Values of 1.96 or less mean there is non-significant kurtosis. Values >1.96 mean there is significant kurtosis, which means significant non-normality.

Repeated Measure anova

Repeated Measure ANOVA was performed using the Mixed Procedure (PROC MIXED) in SAS/STAT®. Because of asymmetric development of the linyphiid web densities estimated during the growing seasons of 1995 as well as 1996, the data exploring procedure revealed that third-degree polynomial models best explained the data sets.

Correlations

The correlations between the estimated vegetation densities and the estimated web densities were tested in relation to the four different growing practices using the Pearson's correlation test. Performing a general linear modelling test by the use of JMP™ (SAS Institute, NC, USA, 1989–2007) showed no interaction between vegetation density and growing practice, which means that the relationship between the estimated vegetation density and the estimated web density is independent of the growing practice. This allows for the pooling of the data from all four different growing practices in a single correlation test.

Structural equation modelling

The relationships between the estimated linyphiid juvenile production, Collembola density in the soil surface, total lower vegetation layer density as well as organic matter and soil water content in the topsoil were analysed using SEM on the basis of a pooled data set from all four different growing systems. The analysis procedure – by choosing the best significant model – follows the guidelines for the statistical programme AMOS 4.0 given by Arbuckle and Wothke (1999).

In the SEM analysis procedure, the model was improved by decreasing the Chi-squared statistic faster than the degrees of freedom. In trying to improve upon a model, we were aware that a modification must only be considered if it makes theoretical or common sense. In contrast to most other statistical tests, the null hypothesis, not the alternative, is the biologically interesting hypothesis, and a probability below the chosen significant level means that the predicted model is wrong and should be rejected (i.e. the null hypothesis should be rejected).

The path coefficients in path analysis are partial regression coefficients, which measure the extent of effect of one variable on another in the path model and are defined as the strength of the relationship. In Amos, the path coefficients are labelled regression weights. Based on the analysis, the standardized regression weights are shown in the path diagram. The model is identified by fixing the path coefficient between each variable and a latent variable to unity, which means a regression weight of one.

Results

Linyphiid webs

The web densities in the wheat-clover bi-crop systems were on average between 200 and 250 webs per square-metre when the densities peaked in 1995 and in 1996, while the estimated average web density peak levels under conventional growing practice with a high input of fertilizers and pesticides (CH) were 100–150 webs per square-metre in both years. In the low-level fertilized conventional growing system with no use of pesticides (CL), the estimated web densities showed peak levels between 150 and 200 webs per square-metre (fig. 2).

The Tukey–Kramer multiple comparisons test performed with the data set for the growing season of 1995 showed that the mean web density level of the unfertilized, bi-crop system (BU) was significantly higher ($P < 0.0001$) than the mean web density level of the high-input, conventional growing system (CH) as well as significantly higher ($P < 0.001$) than the mean web density level of the low-input, conventional growing system (CL). Moreover, the mean web density of the low-level fertilized, bi-crop system (BL) was significantly higher ($P < 0.0001$) than the mean web density level of the high-input, conventional growing system (CH) as well as significantly higher ($P < 0.05$) than the mean web density level of the low-input, conventional growing system (CL). The number of Repeated Measure observations in 1995 was 88.

The Tukey–Kramer multiple comparisons test performed with the data set for the growing season of 1996 showed that the mean web density level of the unfertilized, bi-crop system (BU) was significantly higher ($P < 0.0001$) than the mean web density level

J. Appl. Entomol. 132 (2008) 545–556

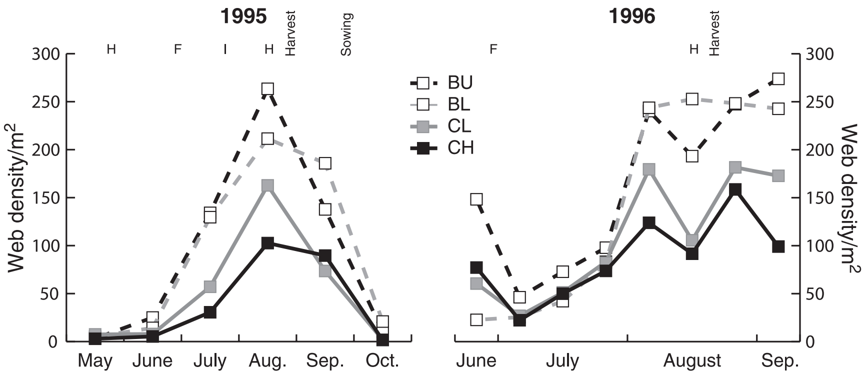

Fig. 2 Mean estimated web densities in the two sampling periods, May–October 1995 and June–September 1996 for the four different growing practices; 'Sowing': Wheat establishing operations in September 1995; 'Harvest': Harvesting operations 17 August 1995 and 23 August 23 1996; F: Fungicide treatments 27 June 1995 and 25 June 1996; H: Herbicide treatments in spring both years as well as before harvest in both 1995 and 1996; I: Insecticide treatment 14 July 1995.

of the high-input, conventional growing system (CH) as well as significantly higher ($P < 0.001$) than the mean web density level of the conventional, low-input growing system (CL). Moreover, the mean web density of the low-level fertilized, bi-crop system (BL) was significantly higher ($P < 0.05$) than the mean web density level of the conventional, high-input growing system (CH). The number of Repeated Measure observations in 1996 was 288.

Linyphiid adults

One-way ANOVA tests showed significant differences in the mean numbers of adult *B. gracilis* ($F_{3,12} = 8.64$; $P < 0.01$; $n = 16$) and *T. tenuis* ($F_{3,12} = 8.82$; $P < 0.01$; $n = 16$) caught in relation to the four different agricultural practices. The Bonferroni test showed that significantly ($P < 0.01$) more adults of *B. gracilis* were found in both bi-crop systems compared with the high-input, conventional growing system (CH), and significantly ($P < 0.01$) more adults of *T. tenuis* were caught in the low-input, bi-crop system (BL) compared with the averages caught in both conventional growing systems (fig. 3).

Vegetation

The mean secondary vegetation layer densities were significantly different between the four different growing systems (one-way ANOVA; $F_{3,12} = 34.61$; $P < 0.001$; $n = 16$). The Bonferroni test showed that the mean secondary vegetation density levels of both bi-crop systems were significant higher ($P < 0.001$) than the mean density level in the high-input, conventional growing system (CH). The mean density level in the unfertilized, bi-crop system (BU) was also significantly higher ($P < 0.01$) than the mean secondary vegetation density level of the conventional, low-input growing system (CL) (fig. 4).

Positive correlations were found between the estimated web densities and the total vegetation densities of the lower vegetation layer for all four wheat-growing systems using the Pearson's correlation test on the basis of the coordinated samplings done in 1995, 1996 and 1997; BU: $r = 0.452$, $P < 0.001$, $n = 59$; BL: $r = 0.333$, $P < 0.05$, $n = 59$; CL: $r = 0.489$, $P < 0.001$, $n = 59$; CH: $r = 0.513$, $P < 0.001$, $n = 58$. The correlation between the estimated web densities in relation to the total lower vegetation layer densities on the basis of a pooled data set representing all four different growing systems was also positive ($r = 0.468$; $P < 0.001$; $n = 235$).

Collembola

The majority of the identified collembolans belong to the species *Isotoma anglicana* Lubbock 1862 (Fjellberg 1980). The mean Collembola densities in the soil surface were significantly different between the four different growing systems (one-way ANOVA; $F_{3,12} = 18.60$; $P < 0.001$; $n = 16$). The Bonferroni test showed that the mean Collembola density in the low-level fertilized, bi-crop system (BL) was significantly higher ($P < 0.001$) than the mean density level in the high-input, conventional growing system (CH), and the mean density in the unfertilized, bi-crop system (BU) as well as the mean density in the low-level fertilized, conventional growing system

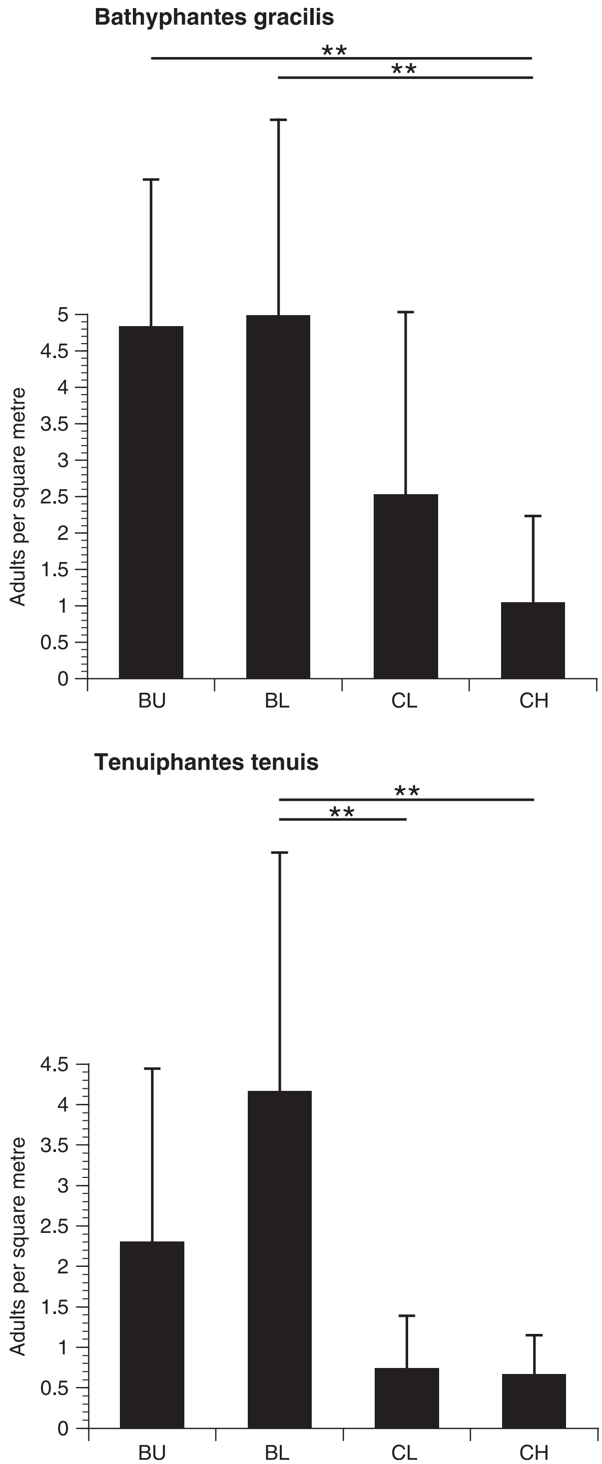

Fig. 3 Estimated mean (mean ± SE) adult densities of *Bathyphantes gracilis* and *Tenuiphantes tenuis* in relation to the four different growing practices. Horizontal bars show significant differences between the mean adult densities in relation to the four different growing practices; *P < 0.05; **P < 0.01; ***P < 0.001.

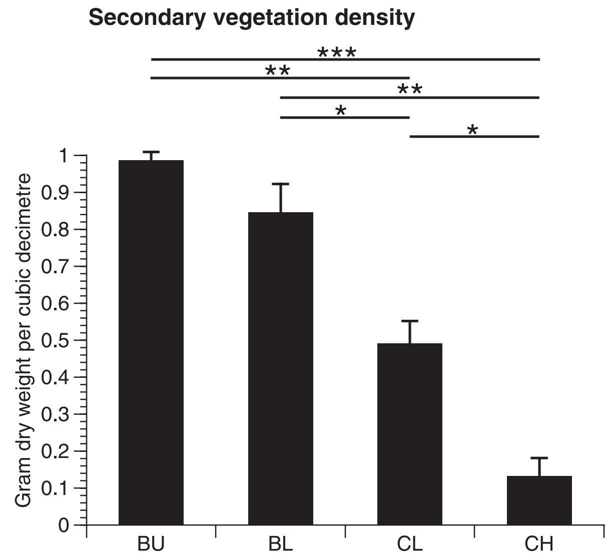

Fig. 4 Estimated mean (mean ± SE) secondary vegetation density as gram dry weight per cubic decimetre in relation to the four different growing practices. Horizontal bars show significant differences between the mean secondary vegetation densities in relation to the four different growing practices; *P < 0.05; **P < 0.01; ***P < 0.001.

(CL) was also significantly higher (P < 0.01) than the mean Collembola density in the high-input, conventional growing system (CH) (fig. 5).

Organic matter and soil water

Both mean values of organic matter content and soil water content in the topsoil were significantly different between the four different growing practices. One-way ANOVA showed a significant difference between the mean values of the organic matter content ($F_{3,12} = 58.45$; $P < 0.001$; n = 16) as well as a significant difference between the mean values of the soil water content ($F_{3,12} = 11.52$; $P < 0.01$; n = 16) in the topsoil in relation to the different growing practices (fig. 5).

The Bonferroni tests showed significantly higher average organic matter content and soil water content in the topsoil with the bi-crop systems compared with the conventional growing systems. The Bonferroni test showed that the mean organic matter content in the experimental plots of both bi-crop systems were significantly higher (P < 0.001) compared with the mean organic matter content in the experimental plots of both conventional growing systems. The Bonferroni test also showed significantly higher (P < 0.01) mean soil water content in the experimental plots of both bi-crop systems

J. Appl. Entomol. **132** (2008) 545–556

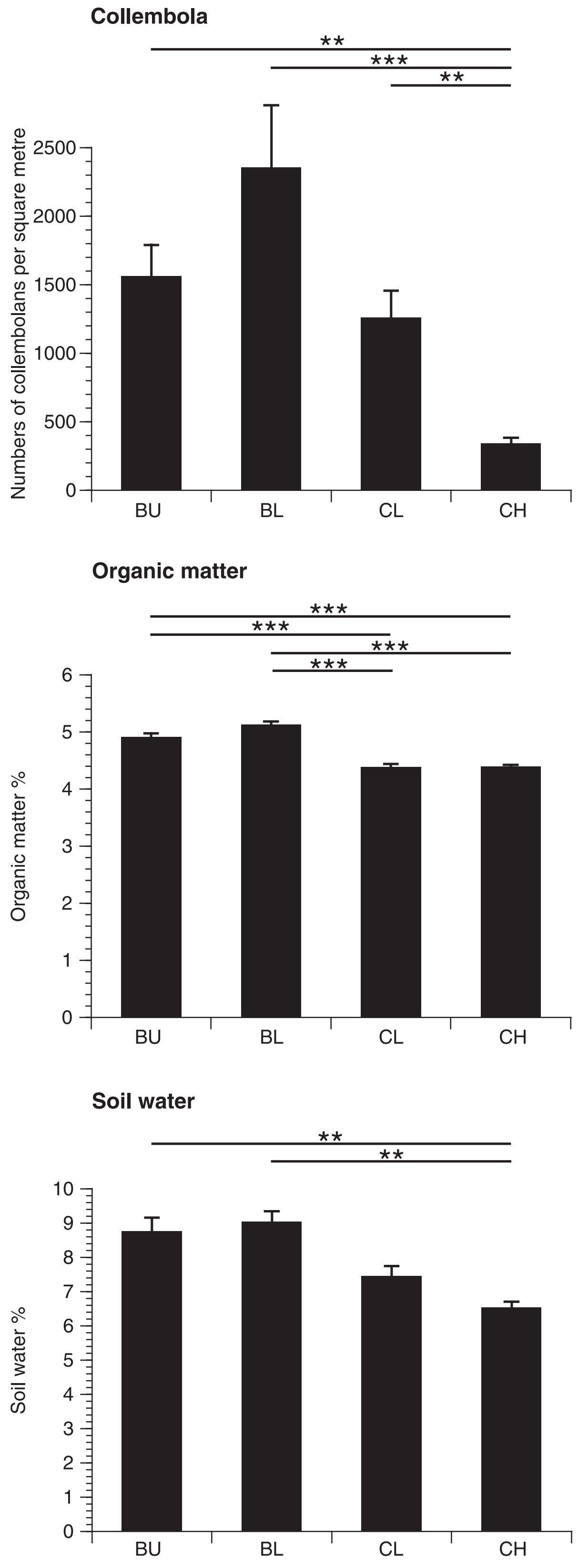

Fig. 5 Estimated mean (mean ± SE) Collembola densities in the soil surface as well as mean (mean ± SE) organic matter and soil water content in the upper five centimetres of the topsoil in relation to the four different growing practices. Horizontal bars show significant differences in relation to the four different growing practices; *P < 0.05; **P < 0.01; ***P < 0.001.

compared with the conventional, high-input growing system (CH) (fig. 5).

Structural equation modelling

In the SEM procedure, the best fitting model was chosen to explain the relationships between the variables 'juvenile production', 'Collembola density' in the soil surface, 'vegetation density' of the lower vegetation layer as well as 'organic matter' and 'soil water' content in the topsoil, which means low Chi-squared statistics compared with the degrees of freedom. Figure 6 shows the path diagram of the relationships between the five variables (χ^2= 8,0; P = 0,16; d.f. = 5; n = 120).

Not surprisingly, the 'organic matter' content in the topsoil was positively influenced by the 'vegetation density' while the 'Collembola density' in the soil surface was positively influenced by the 'organic matter' content. The 'organic matter' content in topsoil also has an indirect influence on the 'Collembola density' as the 'soil water' content in the topsoil is

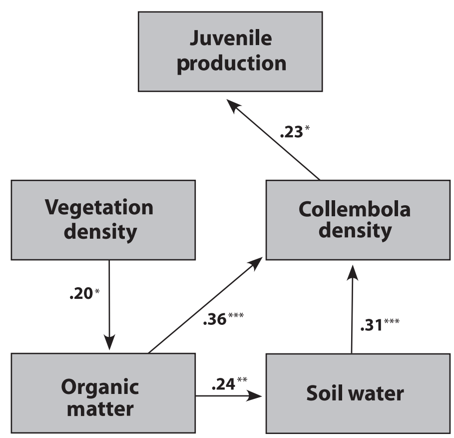

Fig. 6 Path diagram showing the relationship between the estimated linyphiid juvenile production, Collembola density, vegetation density as well as organic matter and soil water content in the topsoil using structural equation modelling (SEM). Model fit: χ^2 = 8.75, d.f. = 5, P = 0.12; n = 120. The figures at each arrow represent the standardized regression weights (the path coefficients).*P < 0.05; **P < 0.01; ***P < 0.001. Regression weights between each variable and a latent variable were fixed to unity in the analysis, but these figures are not shown in the diagram.

dependent on the 'organic matter' content while the 'Collembola density' has a positive influence on the 'juvenile production'.

Discussion

The beneficial effects of the bi-crop technique is evident even though the wheat-clover bi-crop experiment from an agronomic point of view was disappointing because the grain yields with the use of a combination of winter wheat and white clover were significantly lower than the grain yields of conventional wheat production systems (Burke et al. 1998). In their bi-crop experiment in Ireland, the grain yields were relatively stable between years while lower levels of aphids and more earthworms were found in the bi-crop system compared with conventional production systems, which show that bi-crop experiments have interesting preliminary investigation potentials although further research is needed before such a system can be presented to the agricultural community.

In this study, the wheat-clover bi-crop technique and the incorporation of a clover vegetation layer together with the wheat crop plants have shown obvious beneficial effects on the adult numbers of the Linyphiinae species – *B. gracilis* and *T. tenuis* (Harwood and Obrycki 2005). Moreover, the significantly higher linyphiid web density levels of the bi-crop system compared with the mean web density level of the high-input, conventional growing system is convincing. The beneficial effect of the bi-crop technique is mainly based on the integration of the perennial clover plants grown in narrow strips between the wheat crop plants in the cereal fields (Samu 2003; Schmidt and Tscharntke 2005).

The positive correlation between linyphiid web density and vegetation density for all four investigated farming systems can be related to the vegetation as a web attachment substrate (Balfour and Rypstra 1998; Rypstra et al. 1999), which shows that clover and weed plants between the crop plants instead of just bare soil between the crop plants may have a beneficial impact on linyphiid web densities in cereal fields (Altieri et al. 1985; Feber et al. 1998).

Less tillage, more organic matter and higher soil water content seem to increase densities of Collembola in arable fields (Axelsen and Kristensen 2000; Bandyopadhyaya et al. 2002; Miyazawa et al. 2002). The reduced tillage practice and the significantly higher average values of organic matter as well as soil water content in the topsoil with the wheat-clover bi-crop technique compared with the conventional wheat-growing practice seems to have beneficial impacts on the Collembola density.

The detritus food chain is left more or less undisturbed with the bi-crop technique compared with the situation with conventional growing practice where the detritus food chain is much more disturbed and reduced at particularly the soil surface. The relatively intact detritus food chain, and with that the higher Collembola densities, is supposed to be the important basis of the higher densities of the ground-dwelling spiders in the bi-crop system compared with the conventional wheat-growing practice with a high input of fertilizers and use of pesticides.

This is in agreement with Wise et al. (2006), who found higher densities of linyphiid spiders as well as Collembola and Diptera as an effect of the addition of detrital subsidy in field experiments, and Schmidt et al. (2005) showed that organically managed winter wheat fields fertilized with manure and with mechanical weed control enhanced spider density by 62% compared with conventionally managed wheat fields with high fertilization and pesticide treatment levels.

The SEM demonstrates the importance of the detritus food chain (McNabb et al. 2001; Wise et al. 2006) for the linyphiid population build up because the linyphiid juvenile production is influenced by the numbers of collembolans accessible as food animals for the adults. This points to the plant residue decomposition process at the soil surface as being crucial for the population build-up of collembolans and, consequently, of the population build-up of the linyphiid spiders as the organic matter content in the topsoil seems to be a key factor.

By using a bi-crop technique with clover as living mulch, the detritus food chain is left more or less undisturbed. This results in higher organic matter and soil water content in the topsoil to the benefit of the collembolans, which is supposed to further support higher reproductive outputs of the linyphiid spiders compared with the situation under conventional growing regimes with bare soil between the crop plants and a reduced detritus food chain. Under the conventional growing regimes, this results in lower organic matter and soil water content in the topsoil with lower Collembola densities in the soil surface, which is supposed to further result in relatively low reproductive outputs of the linyphiid spiders.

A combination of ecological density estimation techniques and SEM has in this study shown a potential as a powerful data analysis procedure, and similar procedures may give a better understanding of the complexity of agro-ecosystems in the future

J. Appl. Entomol. **132** (2008) 545–556

and in that way support the further development of ecologically sustainable growing techniques.

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References

Alderweireldt M, 1994. Habitat manipulations increasing spider densities in agroecosystems – possibilities for biological control. J. Appl. Entomol. 118, 10–16.

Altieri MA, Wilson RC, Schmidt LL, 1985. The effects of living mulches and weed cover on the dynamics of foliage- and soil-arthropod communities in three crop systems. Crop Prot. 4, 201–213.

Arbuckle JL, Wothke W, 1999. Amos 4.0 User's Guide. SmallWaters Corporation, Chicago.

Axelsen JA, Kristensen KT, 2000. Collembola and mites in plots fertilised with different types of green manure. Pedobiologia 44, 556–566.

Balfour RA, Rypstra AL, 1998. The influence of habitat structure on spider density in no-till soybean agroecosystem. J. Arachnol. 26, 221–226.

Bandyopadhyaya I, Choudhuri DK, Ponge JF, 2002. Effects of some physical factors and agricultural practices on Collembola in a multiple cropping programme in West Bengal (India). Eur. J. Soil Biol. 38, 111–117.

Burke JI, Thomas TM, Finnan JM, 1998. Bi-cropping of winter wheat and white clover. Project Report 4316, Teagasc, Carlow.

Feber RE, Bell J, Johnson PJ, Firbank LG, Macdonald DW, 1998. The effects of organic farming on surface-active spider (Araneae) assemblages in wheat in southern England, UK. J. Arachnol. 26, 190–202.

Fjellberg A, 1980. Identification keys to Norwegian Collembola. Norsk Entomologisk Forening, Oslo.

Harwood JD, Obrycki JJ, 2005. Web-construction behaviour of linyphiid spiders (Araneae, Linyphiidae): Competition and co-existence within a generalist predator guild. J. Insect Behav. 18, 593–607.

Keuls M, Over HJ, de Wit CT, 1963. The distance method for estimating densities. Stat. Neerl. 17, 71–91.

Krebs CJ, 1989. Ecological methodology. Harper & Row, New York.

Marcussen BM, Axelsen JA, Toft S, 1999. The value of two Collembola species as food for a linyphiid spider. Entomol. Exp. Appl. 92, 29–36.

McNabb DM, Halaj J, Wise DH, 2001. Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroecosystems: a stable isotope analysis. Pedobiologia 45, 289–297.

Miyazawa K, Tsuji H, Yamagata M, Nakano H, Nakamoto T, 2002. The effects of cropping systems and fallow managements on microarthropod populations. Plant Prod. Sci. 5, 257–265.

Roberts MJ, 1987. The spiders of Great Britain and Ireland. Volume 2 (Linyphiidae). Harley Books, England.

Rypstra AL, Carter PE, Balfour RA, Marshall SD, 1999. Architectural features of agricultural habitats and their impact on the spider inhabitants. J. Arachnol. 27, 371–377.

Samu F, 2003. Can field-scale habitat diversification enhance the biocontrol of spiders? Pest Manag. Sci. 59, 437–442.

Schierup H-H, Jensen A, 1981. Vejledning i kemisk og fysisk analyse af jordprøver og plantemateriale. University of Aarhus, Denmark.

Schmidt MH, Tscharntke T, 2005. The role of perennial habitats for Central European farmland spiders. Agr. Ecosyst. Environ. 105, 235–242.

Schmidt MH, Thewes U, Thies C, Tscharntke T, 2004. Aphid suppression by natural enemies in mulched cereals. Entomol. Exp. Appl. 113, 87–93.

Schmidt MH, Roschewitz I, Thies C, Tscharntke T, 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. J. Appl. Ecol. 42, 281–287.

Shipley B, 2000. Cause and correlation in biology. Cambridge University Press, Cambridge.

Southwood TRE, Henderson PA, 2000. Ecological methods. 3rd edition. Blackwell Science, Oxford.

Sunderland K, Samu F, 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. Entomol. Exp. Appl. 95, 1–13.

Sunderland KD, Topping CJ, 1995. Estimating population densities of spiders in cereals. In: Arthropod natural enemies in arable land. Proceedings of the First EU Workshop on Enhancement, Dispersal and Population Dynamics of Beneficial Insects in Integrated Agrosystems: 'Estimating population densities and dispersal rates of beneficial predators and parasitoids in agroecosystems' held at the University of Aarhus, Denmark, 1993. Ed. by Toft S, Riedel W, Aarhus University Press, Denmark, 13–22.

Toft S, Vangsgaard C, Goldschmidt H, 1995. Distance methods used to estimate densities of web spiders in cereal fields. In: Arthropod natural enemies in arable land. Proceedings of the First EU Workshop on Enhancement, Dispersal and Population Dynamics of Beneficial Insects in Integrated Agrosystems: 'Estimating population densities and dispersal rates of beneficial predators and parasitoids in agroecosystems' held at the University of Aarhus, Denmark, 1993. Ed. by Toft S, Riedel W, Aarhus University Press, Denmark, 33–45.

Wise DH, Moldenhauer DM, Halaj J, 2006. Using stable isotopes to reveal shifts in prey consumption by generalist predators. Ecol. Appl. 16, 865–876.

Wright S, 1921. Correlation and causation. J. Agr. Res. 10, 557–585.

