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THE WEB-SPIDER COMMUNITY OF SOYBEAN AGROECOSYSTEMS IN SOUTHWESTERN OHIO

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ABSTRACT. We documented the web-spider community in a soybean agroecosystem over the entire growing season in 1990 and 1991 and over the period of peak spider abundance in August of 1993. Simultaneously a number of vegetational parameters were quantified in order to determine the extent to which the spider abundance was correlated with characteristics of the plant community. Web-spider abundance was higher in 1991 than in 1990 or 1993 and lower in 1993 than the other two years. The composition of the community in terms of web-types also differed among years with sheet webs (Linyphiidae, Agelenidae) being much more abundant in 1991 and orb webs (Araneidae) more abundant in 1990. In 1991, spider abundance was correlated with specific vegetation characteristics which suggests that the availability of habitat was important to spider colonization and establishment in that year. However, in 1990 spider abundance was not correlated with any of the vegetation characteristics we measured. The late season spider density was positively correlated with weed biomass and the damage inflicted on the soybean leaves by herbivores was negatively correlated with the number of web-spiders across the three years. These data suggest that the web-spider community responds to some aspects of the plant community and that they have the potential to impact plant production by reducing the action of herbivores.

Spiders are common generalist predators on arthropods in many agricultural systems. In spite of this fact, little data exist on their activities in these systems (Riechert & Lockley 1984; Nyffeler & Benz 1987; Young & Edwards 1990; Wise 1993). Because spiders are generalist predators and most efforts to implement biological control have focused on predator or parasitoid interactions to reduce the impact of specific pests, spiders have not been considered seriously (Riechert & Lockley 1984; Nyffeler & Benz 1987). In addition, spiders have relatively long generation times and agricultural habitats are frequently disturbed by activities such as plowing and planting, which means that a large proportion of the spider community has to be re-established each season (Riechert & Lockley 1984; Young & Edwards 1990). It is not yet clear how predictable the spider community is from year to year and what factors might influence it most directly.

Plants are important modifiers of the microclimate for arthropods, specifically by moderating temperature and humidity extremes and by providing a more complex three-dimensional habitat (Cloudsley-Thompson 1962). The changes plants cause are dramatic in strongly seasonally systems like agricultural fields where areas are specifically managed to proceed from no vegetation to a continuous cover of vegetation in a few months. As crop plants develop, the fields gradually become more hospitable to colonization by spiders and other arthropods because the plants provide structure, shade and help maintain moisture. Web-building spiders are particularly dependent on vegetation to provide suitable web-attachment sites (Greenstone 1984; Rypstra 1986; Uetz 1991). Data suggest that spider colonization via aerial dispersal peaks early in the growing season (Bishop 1990; Bishop & Riechert 1990) so developmental rate and spacing pattern of crop plants should influence the establishment of the spider community in agroecosystems (Ferguson et al. 1984; Stinner & House 1990).

In the United States, 262 species of spiders have been found in soybean (*Glycine max* (L.) Merrill) fields (Young & Edwards 1990). In a given area, the number of spider species is likely to be less than that number, but soybeans typically contain one of the most diverse communities seen in any agricultural crop (LeSar & Unzicker 1978; Young & Edwards 1990). Culin & Rust (1980) reported that the foliage community of spiders in soybeans responded across the season to habitat space, a measure of plant development, whereas the ground dwelling spider community changed less over the season. Further evidence of the response of spiders to the soybean vegetation is apparent in comparisons among different cropping systems. Typically more foliage-dwelling spiders have been found in fields where the plants were closer together and the cover more continuous than in other fields (Sprenkel et al. 1979; McPherson et al. 1982; Ferguson et al. 1984).

In this study we focused on specific aspects of how the plant abundance and structure might be related to the web-spider community that developed in soybeans. We attempted to determine how closely the spiders tracked vegetation development in this system by monitoring both spiders and plants weekly for two full seasons. In a third season, we collected data only at the time of peak web-spider and vegetational abundance in order to assess how predictable the web-spider guild composition was from year to year and to determine which vegetational characteristics might be most closely tied to spider abundance across years.

METHODS

Study area.—The study was conducted in soybean monoculture plots located at the Miami University Ecology Research Center, three miles north of Oxford, Butler County, Ohio, USA (Kemp & Barrett 1989). Each plot measured 60 × 70 m and contained 82 rows of soybeans planted in an east-west direction. Experimental plots were bordered on all sides by a 15 m mowed grass strip. Four plots were randomly selected from an array of 12 in 1990 and three plots were selected from that array in 1991 and 1993.

Herbicides were applied to all plots in all years. The pre-emergence herbicides, Lorox Plus® (linuron plus chlorimuron; 0.51 kg active ingredient/hectare) and Dual 8E® (metolachlor; 1.4 kg active ingredients/hectare), were applied to control for broadleaf and grassy weeds, respectively, in all three years. In 1991 and 1993, the post-emergence herbicide, Poast Plus® (sethoxyoim plus dash; 0.28 kg active ingredients/hectare) was applied three weeks after planting to control grassy weeds. All herbicide treatments were applied before we began sampling the plots. No insecticides were applied to the plots in any year.

Plant characteristics.—Vegetation development was monitored weekly in each plot. We measured the height and width of five plants selected by generating random coordinates which determined meter points in a plot each week from three weeks after plant emergence until harvest. In order to obtain a measure of vertical leaf distribution and therefore the availability of possible web attachment points on the soybean plants, we placed a meter stick through the center of each of the five plants and recorded the height of each leaf touching the stick. Foliage height diversity (H′) was then calculated from the leaf height measurements where $H' = -\Sigma p_i \ln p_i$ (p_i = the proportion of the total number of leaves within a 10 cm interval of soybean plant height) (Shannon & Weaver 1949).

Total above ground production was measured just before the soybeans began to senescence (stage R6 as designated by Fehr & Caviness 1977) in all three years. On 7–10 September 1990, 16–20 August 1991 and 1993 four locations were selected randomly within each plot. One row meter of the soybean plants was clipped at the soil surface and collected. In addition the weeds in the area extending to the center point between rows on either side were clipped and collected. Plants were placed in a drying oven at 80 °C for at least seven days and then weighed.

We assessed the cumulative damage inflicted by leaf chewing insects to soybean plants over the season by measuring leaf damage at the end of the season. Two sites in each plot were selected by generating random number coordinates. In 1990 on 10 September, we traced 10 leaflets onto index cards at each site. On 24 August in 1991 and 1993, we traced 12 leaflets at each site. Leaflets areas were then determined to the nearest 0.1 cm^2 using a calibrated grid.

Spiders.—We monitored the web-spider community in the soybean plots by sampling four 1 m row lengths in each plot each week from the third week after plant emergence (early June) until harvest (late September) in 1990 and 1991 and from mid-season (mid July) to harvest in 1993. Specific row sections to be sampled were determined using different randomly generated coordinates each week. At each site, the plants and soil were visually searched for web-spiders between 0750–1050 h when dew made the webs most visible. Most web-spiders present in the fields were juveniles, which were difficult to identify, especially without collection. Therefore, web-spiders were classified by web type (sheet, orb, or tangle). Sheet-web weavers (Linyphiidae, Agelenidae) build webs that are characterized by a dense horizontal plane of silk frequently with a barrier web consisting of a tangle of silk surrounding the sheet to some degree. Orb-wel weavers (Araneidae) consist of a circular plan of silk spirals with supporting spoke strands radiating from the hub. Tangle-web weavers (Theridiidae) build a three-dimensional and somewha

Table 1.—The soybean growing season was separated into three time periods based on the developmental stage of the plants.

Year	Early	Middle	Late
1990	10 July–23 August	24 August–20 September	21 September–13 October
1991	5 July–5 August	6 August–2 September	3 September–28 September
1993	28 June–24 July	25 July–28 August	29 August–25 September

irregular mesh of strands connecting the vegetation.

Data analysis.—The soybean season in Ohio typically encompasses a four-month period from planting to harvest. The period of study shifted each year due to weather differences and the timing of planting. For ease of comparison relative to the maturity of the plants, we divided each year into early, middle and late month-long time periods (Table 1). For years in which we had data for the entire season, a mean for each plot was generated for each of the three time periods. We then tested for differences between years and season nested in year using a repeated measures analysis of variance. Comparisons of just the late season information across the three years were made using a one-way analysis of variance. The Tukey-Kramer Test was used to make pairwise comparisons among years. Mean spider abundance in the late season was regressed on those vegetation parameters that differed across all three years in an attempt to explain yearly variation in spider abundance. The 1990 and 1991 seasonal data were analyzed separately to dissect

Table 2.—Summary of vegetation data from the soybean fields (Mean ± SD). ANOVA statistics for plant height, width, and H′ are results of repeated measures test for differences among years and season nested in year. Statistics for biomass and leaf damage are from one-way ANOVA.

	1990	1991	1993
Plant height (cm)			
Early	47.1 ± 2.9	41.2 ± 4.6	51.2 ± 3.7
Middle	74.9 ± 2.2	89.7 ± 2.4	92.6 ± 3.2
Late	72.5 ± 1.4	94.0 ± 2.0	95.2 ± 2.1
	year, season (year): $F = 168, 49.8$; $df = 2,6$; $P < 0.05$		
Plant width (cm)			
Early	47.5 ± 3.2	44.7 ± 3.3	42.3 ± 3.1
Middle	69.1 ± 1.7	65.8 ± 2.2	68.0 ± 2.3
Late	41.8 ± 3.1	61.3 ± 4.7	64.7 ± 5.7
	year, season (year): $F = 33.7, 7.9$; $df = 2,6$; $P < 0.05$		
Foliage height diversity (H′)			
Early	1.44 ± 0.05	1.48 ± 0.03	1.54 ± 0.06
Middle	1.87 ± 0.03	1.88 ± 0.04	1.92 ± 0.05
Late	1.27 ± 0.14	1.67 ± 0.10	1.74 ± 0.12
	year, season (year): $F = 16.06, 10.2$; $df = 2,6$; $P < 0.05$		
Soybean biomass (g)			
Late	174 ± 32	356 ± 89	423 ± 97
	year: $F = 32.45$; $df = 2$; $P < 0.05$		
Weed biomass (g)			
Late	503 ± 153	987 ± 102	68 ± 49
	year: $F = 46.13$; $df = 2$; $P < 0.05$		
Leaf damage (%)			
Late	5.9 ± 0.6	2.2 ± 0.4	26.7 ± 4.5
	year $F = 56.56$; $df = 2$; $P < 0.05$		

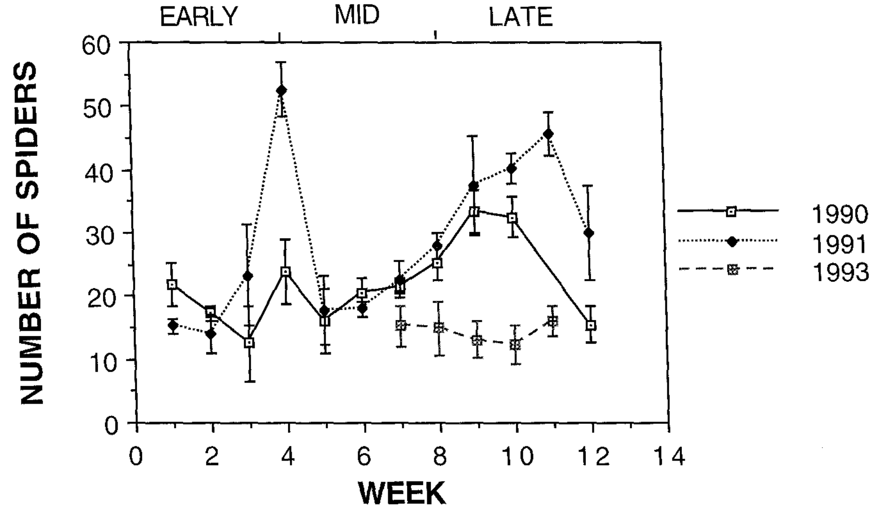

Figure 1.—Spider abundance (per four one-meter row sections) in soybean plots over the entire growing season in 1990 and 1991 and the latter part of the season in 1993 (Mean ± SD).

how closely the spiders tracked the changes in vegetation. Weekly values of the number of spiders were regressed on weekly values for vegetation height, width, and foliage height diversity.

RESULTS

Vegetation.—Soybean plant size differed significantly among years but those differences were only really apparent in the middle and late portions of the season so there was a significant seasonal effect as well (Table 2). Plants were larger and more complex (as measured by foliage height diversity) in 1991 and 1993 than they were in 1990 (Table 2). Likewise, the above ground soybean biomass of one row meter at the peak of lushness (R6) was significantly greater in 1991 and 1993 than it was in 1990 (Table 2). The above ground biomass of weeds surrounding one meter of soybean plants weeds also varied among years (Table 2). The Tukey-Kramer Pairwise Comparisons Test revealed that there was greater weed biomass in 1991 than in 1990 or 1993 and weed biomass was higher in 1990 than it was in 1993 (Table 2). The proportion of each leaflet damaged was also different from year to year (Table 2). Chewing insects damaged the soybean plants much more dramatically in 1993 than in 1990, and plants in both 1990 and 1993 received more damage than in 1991 (Table 2) (Tukey-Kramer Test, $P < 0.05$).

Spiders.—There were significantly more web spiders found in 1991 than in 1990 across the whole season (Fig. 1) (repeated measures of year, season (year): $F = 9.81, 6.15$, $df = 1, 5$, $P < <0.05$). There was considerable overlap in the early and mid-season numbers but the abundances clearly separated by year in the late season (Fig. 1). We did not collect early or mid-season data for 1993, but there were significantly fewer spiders in the late season of that year than in the late season of either of the other two years (Fig. 1) ($F = 60.91$, $df = 2$, $P < 0.05$).

Sheet webs were the most abundant web type in the soybean fields and, at the time of peak spider abundance in the late season, they comprised over 40% of the spiders we observed in all three years (Fig. 2). Sheet webs were significantly more abundant in the 1991 season than they were in 1990 (Table 3). There were no seasonal differences in sheet web abundance in 1990 or 1991 (Table 3). If we compare the late season data from all three years, there were significantly more sheet webs in the fields in 1991 than in the other two years (Table 3) (Tukey-Kramer Test, $P < 0.05$). More than 75% of the sheet-web builders in the plots in all three years belonged to five species (Table 4).

Orb webs were second in abundance to sheet webs in 1990 and 1993 when they comprised more than 25% of the late season community, but they were very uncommon in 1991 (Fig. 2). Unlike sheet-web spinners, the orb-web weavers were significantly more abundant across the season in 1990 than they were in 1991 (Table 3).

Table 3.—Abundances of the three common web types in soybean fields (Mean ± SD). ANOVA statistics are results of repeated measures test for differences between 1990 and 1991, and for season nested in year. Late season data indicated with "*" were significantly different from other years by Tukey-Kramer Pairwise Comparison Test ($P < 0.05$).

	1990	1991	1993
Number of sheet webs			
Early	10.9 ± 6.0	23.0 ± 4.5	–
Middle	11.6 ± 3.1	18.0 ± 3.1	–
Late	11.5 ± 2.7	26.6 ± 3.8*	6.3 ± 4.0
year, season (year): $F = 38.27, 1.7$; $df = 1,5$; $P < 0.05, P > 0.1$			
Number of orb webs			
Early	5.6 ± 1.3	3.7 ± 1.4	–
Middle	5.7 ± 1.4	2.0 ± 0.3	–
Late	11.1 ± 2.2*	3.9 ± 0.5	3.3 ± 1.2
year, season (year): $F = 50.13, 10.39$; $df = 1,5$; $P < 0.05$			
Number of tangle webs			
Early	0.8 ± 1.0	0.7 ± 0.6	–
Middle	1.0 ± 0.5	0.3 ± 0.3	–
Late	2.9 ± 0.7	4.6 ± 0.8	0.9 ± 1.0*
year, season (year): $F = 0.69, 22.21$; $df = 1,5$; $P > 0.1, P < 0.05$			

Additionally there was a significant seasonal increase in the number of orb webs that we were able to find in 1990 (Table 3). In a comparison of late season data of all three years, orb web abundance was significantly higher in 1990 than it was in either of the other two years (Table 3) (Tukey-Kramer Test, $P < 0.05$). Five species comprised better than 75% of the orb-web weavers that we observed in this habitat (Table 4).

Tangle-web weavers were least abundant of the web-spinners, comprising less than 15% of the web-spider community in the soybean fields in the late season of all three years (Fig. 2). There was not a significant difference between the abundance of tangle web weavers in 1990 and 1991 (Table 3). However, the abundance of spiders building tangle webs was significantly greater later in the season than it was in the early or middle portions in those years (Table 3). In a comparison of the late season data on tangle weaver abundance, there were significantly fewer in 1993 than in the other two years of this study (Table 3). Four species of tangle-weavers were collected in all three years (Table 4).

Spiders in relation to vegetation.—Total web-spider abundance across the season was correlated with many of the vegetation parameters in 1991, but was not correlated with any of these parameters in 1990 (Table 5). In 1991, the strongest correlation was between soybean plant width and web-spider abundance. However, foliage height diversity, and plant height were also significantly correlated with spider abundance in that year (Table 5).

Table 4.—List of most common spider species found in the soybean fields categorized by web type.

- Sheet-web weavers
  - Agelenidae
    - *Agelenopsis pennsylvanica* (C. L. Koch)
  - Linyphiidae
    - *Frontinella pyramitela* (Walck.)
    - *Meioneta micaria* (Emerton)
    - *Tennesseellum formicum* (Emerton)
    - *Microlinyphia pusilla* (Sundevall)
- Orb-web weavers
  - Araneidae
    - *Argiope aurantia* Lucas
    - *A. trifasciata* (Forskal)
    - *Cyclosa conica* (Pallas)
    - *Neoscona arabesca* (Walck.)
    - *Tetragnatha laboriosa* Hentz
- Tangle-web weavers
  - Theridiidae
    - *Achaearanea tepidariorum* (C. L. Koch)
    - *Theridion frondeum* Hentz
    - *T. neshamini* Levi
    - *Theridula opulenta* (Walck.)

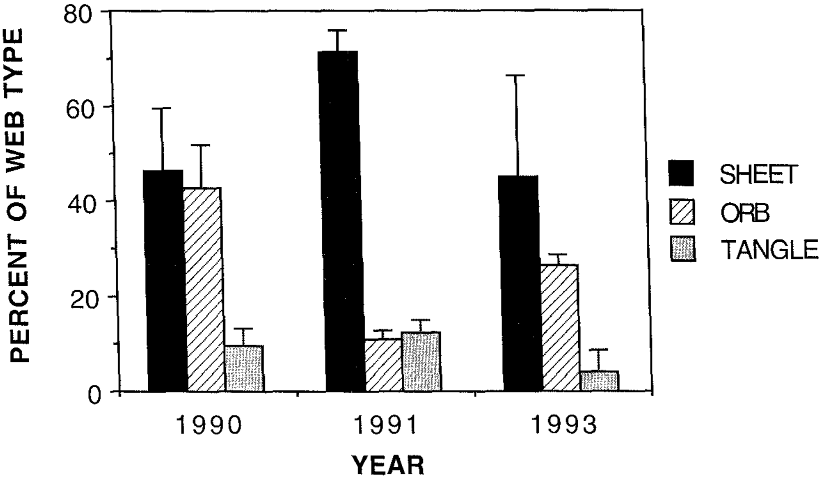

Figure 2.—The relative abundance (percent of all web-spiders found) of sheet, orb, and tangle webs that comprised the web-spider community in soybeans during the late season of three years.

The relative amount of weedy vegetation, leaf damage (which is a measure of the activity of herbivores) and web spiders in the late season across the three years of this study appear to be related. Weed abundance was a vegetation parameter that was different in all three years, and it had a strong positive correlation with spider abundance across years (Fig. 3) ($R^2 = 95.5$, $P < 0.05$). Leaf damage also differed among all years and it was negatively correlated with spider abundance (Fig. 4) ($R^2 = 79.5$, $P < 0.05$). Because of the strong correlation between weeds and spiders and between spiders and leaf damage, leaf damage was also negatively correlated with weed abundance in this data set ($R^2 = 74.0$, $P < 0.05$).

DISCUSSION

The phenology of web-spiders in these Ohio soybean fields was similar in many respects to that observed in other north temperate studies (LeSar & Unzicker 1978; Culin & Rust 1980; Culin & Yeargan 1983; Ferguson et al. 1984). The variation among years is interesting in that the overall abundance was different in each of the three years and that difference is not reflected

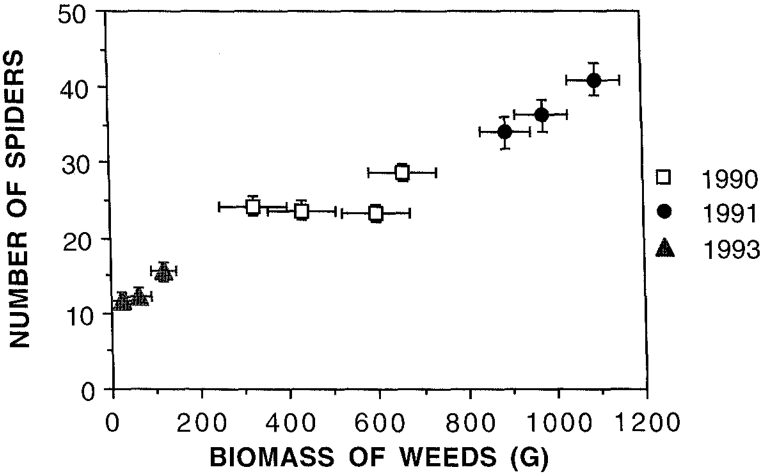

Figure 3.—The mean number of web spiders (per four one-meter row sections) found in the soybean fields late in the season as a function of the biomass of weeds surrounding one row meter.

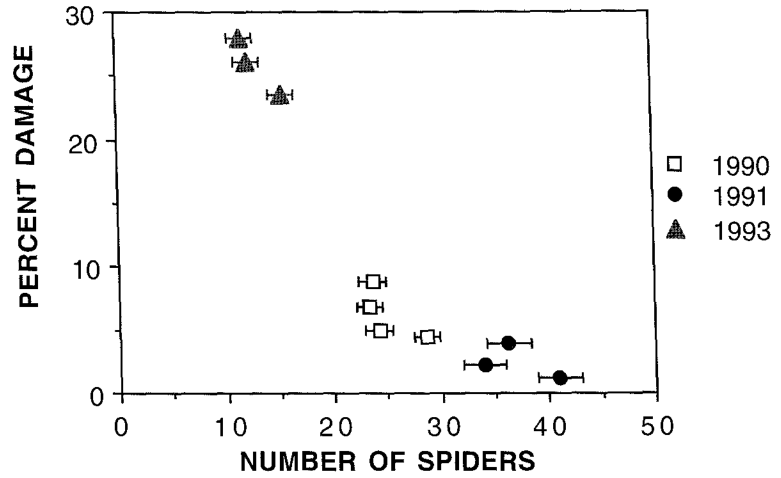

Figure 4.—Leaf damage (% removed by pest insects) experienced by soybean leaves as a function of the number of web-spiders (per four one-meter row sections) found in each field over three years.

by parallel differences in the web types we observed. For example, the highest overall spider abundance was in 1991 when sheet webs dominated the community but orb webs were much more abundant in 1990 (Fig. 2). LeSar & Unzicker (1978) observed that both *Tetragnatha laboriosa,* an orb weaver, and *Microlinyphia pusilla,* a sheet-web weaver, were more abundant in a dry year than they were in a second wetter year and they attributed this differences to a negative effect of rainfall on web spinners. The sheet-web weavers at our site appeared to follow that pattern in that they were much more abundant in 1991, the driest of the three years studied (J. Klink pers. comm.). However, orb weavers, including *T. laboriosa,* were most abundant in 1990 (Fig. 2) which was the wettest of the three years under study (J. Klink pers. comm.). In 1991, sheet-web weavers were very abundant early in the season in relation to any other web type in any year (Table 3). It must be that, for some reason, they were able to disperse in precisely when microhabitat conditions were suitable and establish themselves in the fields early in that year. Since their webs are frequently three-dimensional and require multiple attachment sites, high sheet web densities could have inhibited the colonization of orb-weavers.

The lower numbers of spiders and differences in spider types present in the fields in 1990 than compared to 1991 may, in part, be due to the time of planting. The soybean season was about two weeks later in 1990 that in the other years (Table 1). Since colonization occurs largely by ballooning and the greatest peak of ballooning is observed early in the summer (Bishop & Riech-

Table 5.—Correlations between plant characteristics and web-spider abundance in soybean agroecosystems in 1990 and 1991.

Variable	Sign	*R*	*df*	*P*
1990				
Height	+	0.234	43	>0.1
Width	+	0.077	43	>0.1
Foliage height diversity	+	0.234	43	>0.1
1991				
Height	+	0.491	47	<0.01
Width	+	0.650	47	<0.01
Foliage height diversity	+	0.565	47	<0.01

ert 1990), more potential colonizers would have found suitable habitat in 1991 than in 1990. Likewise, the timing of planting may have coincided with the ballooning of sheet-web weavers to lead to a greater establishment of those spiders in that year. The season in 1993 was even earlier (Table 1) and the plants developed normally (Table 2), so this explanation for annual differences does not explain the overall low spider abundance observed in that year.

The specific development of the web-spider community was more closely aligned with various vegetational measurements in 1991 than in 1990 (Table 5). In many cases, the complexity of the habitat has been related to spider abundance (Greenstone 1984; Rypstra 1983, 1986; Döbel et al. 1990; Gunnarsson 1990; Uetz 1991). Yet in 1990 when overall spider abundance was lower, there were no significant correlations between spider abundance and plant structure (Table 5). The lack of any such correlations, might suggest that the habitat was not saturated, i. e., that there were suitable unused web sites. Alternatively, since sheet webs comprised such a large proportion of the web-spider community in 1991, it may be that our measures of vegetational complexity were better measures of habitat suitability for sheet-web weavers than for all web spiders (Fig. 2). One complication is that the overall spider community appeared to respond quite strongly across years to weed abundance which was also highest in 1991 (Fig. 3), yet our measures of vegetational heterogeneity focused specifically on the soybean plants and did not reflect changes in the developing weed community. The tighter correlations we observed in 1991 in comparison to 1990, may mean that sheet-web weavers were more dependent on the soybean plants themselves for web sites than the other spiders we observed.

Previous studies have demonstrated that spider numbers can be manipulated by altering the habitat structure available to them (Robinson 1981; Rypstra 1983; Carter & Rypstra 1995). Likewise, in no-till soybean systems, which tend to be more weedy than conventionally tilled fields, the greater diversity and abundance of beneficial arthropods, including spiders, have been attributed to the greater structural diversity of the plant community (House & Stinner 1983). Ferguson et al. (1984) found greater spider numbers and diversity in soybean fields that were planted closer together and disturbed less. Our data support those studies and suggest that high weed abundance is the basis for a more dense community of web spiders (Fig. 3).

It has been demonstrated that spiders can reduce the herbivory experienced by plants (Riechert & Bishop 1990; Carter & Rypstra 1995). The strong negative correlation between spider abundance and leaf damage we observed suggests that the spiders were having an impact on the action of herbivores in these fields as well (Fig. 4). We believe that weed abundance allowed a more dense community of spiders (Fig. 3) and that the reduction in leaf damage is due to the direct and indirect effects of the spiders on the herbivores. In experiments with introduced web-spiders in these same soybean fields, we observed a negative correlation between the biomass of prey killed by spiders and leaf damage experienced by plants in localized areas (Carter & Rypstra 1995). Therefore we think that it is likely that the differences in damage we observed across years in this study are due to differences in the spider community. However, one cannot ignore the correlation between weed biomass and leaf damage. Weeds may offer polyphagous pests an alternative food source and, in that way, reduce their dependence on the crop plants.

The results of studies on the interaction of weeds, foliage pest species, and crop plants are mixed, with some pest species inflicting more damage to the crop plants when weeds are abundant and some pest species inflicting less (Hammond et al. 1987; Stinner & House 1990). However, more frequently it has been suggested that the reduction in pest damage in no-till, and therefore weedy, agroecosystems is due to increased predation on or parasitism of herbivorous insects (Speight & Lawton 1976; House & Stinner 1983; Pavuk & Stinner 1992). Clearly more work is critically needed to uncouple these effects in order to understand the relationship between spiders, their prey and the plants in agroecosystems.

In summary these data suggest that agricultural systems contain highly variable dynamic web spider communities in which the composition parameters are related to vegetation development in some years. More information on the specifics of colonization and establishment of different spiders and their preferred plant associations are critical to understanding this system. These data underscore the importance of understanding such interactions since it is becoming increasingly clear that spiders are important predators that can influence the action of pest insects in agroecosystems.

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