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Composition, abundance and pest control potential of spider communities in agroecosystems: a comparison of European and US studies

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Abstract

Current knowledge of spiders in agroecosystems (excluding tree crops) reported in European and US literature is discussed comparatively, in an attempt to relate spider community structure to pest control potential.

The spider fauna of agroecosystems in the northern-temperate zone of Europe is strongly dominated by small linyphiid spiders that capture tiny insects in their sheet webs, including large numbers of pest aphids. In the US, spider guild structure is more complex, and hunters (especially, Oxyopidae, Salticidae, Clubionidae, Thomisidae, and Lycosidae), that have broader diets (including lepidopteran and heteropteran pests), numerically prevail in many locations. Spider populations increase to high densities (2–600 m⁻²) in European field crops, but densities are typically much lower (0.02–14 m⁻²) in US annual crops. Agroecosystem spiders, in both Europe and the US, feed rather infrequently, but they contribute to pest control as part of larger assemblages of natural enemies, and there is potential for increasing their density and impact in both continents.

Many of the differences between continents in spider guild structure, density and feeding patterns highlighted in this paper are likely to be attributable to climatic differences. Most of the US data originate from more southern latitudes (i.e., subtropical and Mediterranean climates) with distinctly higher mean annual temperatures compared to the European study areas, which are in the northern-temperate zone. Spider communities may respond to climate directly, and also indirectly via food availability and antagonists. In addition, differences in crop structure and cultural practices (including habitat diversification and the provision of ground cover) could influence spider density and community organisation. Mean farm size is an order of magnitude less in Europe than in the US and this is likely to be associated with greater habitat diversity, which is known to increase spider abundance.

Currently, there is a dearth of field studies from southern Europe (Mediterranean climate) and the northern regions of the US (humid continental climate). The few data available from such regions indicate that the patterns of spider predation may differ less between the two continents if sufficient study areas with similar climatic conditions could be compared. The conclusions

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in terms of biological control are, however, widely applicable, because a large proportion of the productive agricultural land area of Europe is located in more northern latitudes and the reverse is true in the US.

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1. Introduction

Spiders are among the most abundant invertebrate predators in terrestrial ecosystems (Turnbull, 1973; Wise, 1993). Most spiders feed primarily on insects and secondarily on other spiders (Nentwig, 1987; Riechert and Harp, 1987; Nyffeler, 1999). Very rarely non-arthropod prey (including earthworms, gastropods, and small vertebrates) are captured by some spiders to supplement their arthropod diet (Foelix, 1996; Nyffeler and Symondson, 2001; Nyffeler et al., 2001). Because of their high abundance and predominantly insectivorous feeding habits, spiders are suspected to play an important predatory role in agroecosystems, woodlands, and other terrestrial ecosystems (Nyffeler and Benz, 1987; Nyffeler, 2000a,b). They are one of the major groups of generalist predators that are needed in the development of efficient, sustainable, low-input agricultural systems (Ekschmitt et al., 1997). Assessments of the ecological importance of spiders have been undertaken mainly in Europe and the US (Whitcomb, 1974; Luczak, 1979; Nyffeler, 1982; Riechert and Lockley, 1984; Marc et al., 1999; Rypstra et al., 1999; Samu et al., 1999; Sunderland and Greenstone, 1999; Toft, 1999; Uetz et al., 1999; Wise et al., 1999). In the following, findings from research on spiders in European and US agroecosystems (excluding top fruit and forestry) are discussed comparatively, with the aim of understanding global patterns of spider predation.

2. Methods

Hundreds of reports on agroecosystem spiders published in scientific journals and books, and in unpublished theses, were searched for relevant information. The search also made use of reviews by Nyffeler (1982), Riechert and Lockley (1984), Sunderland (1987), Young and Edwards (1990),

Breene et al. (1993) and Nyffeler et al. (1994a,b). Mean annual temperatures (in °C) at the study sites relevant to published investigations of agroecosystem spiders in Europe and the US have been taken from: <http://www.worldclimate.com>. Data on soil temperatures at Wellesbourne, UK, were provided by Horticulture Research International, and soil temperature data (in °F converted to °C) were also obtained from The University of Kentucky Agricultural Weather Station at Lexington, and from the Texas A&M University Research and Extension Center at Stephenville. Data on mean farm size were taken from the European Commission (Report on the Agricultural Situation in the European Union, OOPEC, Luxembourg, 1998) for Europe, and from The National Agricultural Statistics Service, USDA (<http://www.usda.gov/nass/nassinfo/nassinfo.htm>) for the US. Information on the proportion of cropland under conservation tillage in the US came from “Conservation tillage numbers plow conventional acres under” published in Purdue News in February 1998 (<http://news.ans.purdue.edu/UNS/html4ever/9802.Evans.notill.html>), whilst equivalent data for Europe came from “Conservation Agriculture in Europe” published by the European Conservation Agriculture Federation (<http://www.ecaf.org/English/First.html>). Data on the geographical range of imported fire ants were obtained from websites of the United States Department of Agriculture (<http://www.aphis.usda.gov>), the Arizona Department of Agriculture (<http://www.agriculture.state.az.us>), and the Virginia Department of Agriculture and Consumer Services (<http://www.vdacs.state.va.us>). The interest was not in taxonomic comparisons, but rather to determine if the ecological structure (guild structure, density, diet) and pest control potential of spider communities were equivalent on the two continents. To this end, species should have been assigned to guilds, but data were insufficient (Uetz et al., 1999). Therefore, whilst recognising the limitations of the approach, spider families were

used as guilds, and differentiation was mainly in relation to foraging strategy and vertical location. For example, many species of Linyphiidae that occur in crops utilise sheet webs located on the ground or a few centimetres above it (Thornhill, 1983; Sunderland et al., 1986a; Alderweireldt, 1994), Lycosidae hunt on the ground and do not make webs (Ford, 1978), but Oxopidae hunt actively on vegetation and do not use webs (Nyffeler et al., 1992a).

There is a dearth of information from southern European Countries, such as Spain, Portugal, Greece and Italy. For convenience and brevity we refer to other studies as relating to “northern-temperate Europe”, but this should be read as including Scandinavia. (e.g. Denmark, Sweden, Norway, Finland), western countries (e.g. France, Belgium, Holland, UK), germanic and central European countries (e.g. Germany, Austria, Switzerland, Poland) and some former communist countries (e.g. Hungary, Czech Republic, Slovakia). In the case of the US, a latitude of approximately 40°N marks the dividing line between northern and southern states.

3. Spiders in European field crops

3.1. Taxonomic composition

European crops are inhabited by a large number of different spider species, mainly from the families Linyphiidae, Lycosidae, Araneidae, Tetragnathidae, and Theridiidae (Luczak, 1979; Nyffeler, 1982; Sunderland, 1987; Hänggi et al., 1995). The spider fauna in European field crops is largely dominated by Linyphiidae (Table 1), many species of which build horizontal sheet webs. Hunting spiders (i.e., those foraging without the use of a web) are of less importance in most locations (overall mean = 14.2% of all spider individuals, $N = 40$ studies). Spiders live on plants as well as on the ground (Luczak, 1979; Nyffeler, 1982), but usually >90% of all spider individuals are found near the ground (Geiler, 1963; Nyffeler, 1982), and 56% of 109 species in UK cereals were confined to the ground and were never caught on plants during 667 sampling occasions (Sunderland et al., 1988).

Ground-dwelling spiders of the family Linyphiidae, most of which are small (1–3 mm long) web-building species, strongly dominate (Table 1). In western Eu-

rope (UK, France, Belgium) and in Germany, the percentage of linyphiids in the spider fauna is very high (93–99% of all spider individuals), which has been verified with several different sampling methods (D-vac, photoelector, pitfall traps, etc.) (e.g., Dinter, 1995). Table 1 suggests that Linyphiidae are somewhat less dominant in Switzerland, Austria and eastern Europe. The species identity of the dominant linyphiids is uniform throughout large parts of Europe, with a few species such as *Oedothorax apicatus*, *Erigone atra*, *Erigone dentipalpis*, and *Lepthyphantes tenuis* usually dominating numerically (Nyffeler, 1982; Dinter, 1996; Sunderland, 1996; Blick et al., 2000). Within crops, wolf spiders (Lycosidae) are more numerous towards the field edge than at the centre (Holland et al., 1999), whereas linyphiids are uniformly distributed at the field scale but aggregate to prey-rich patches at the microscale (Harwood et al., 2001a). Linyphiids often dominate the arachnofauna in non-crop habitat at the edge of crop fields in the UK (White and Hassall, 1994; Houghton et al., 1999), but in Hungary (Tóth and Kiss, 1999) and Austria (Kromp and Steinberger, 1992), lycosids and other non-lynyphiid spiders dominate. Linyphiids capture prey with small horizontal sheet webs spun over small depressions on the ground, but lycosids are medium-sized (4–6 mm long) hunters that forage on the soil surface without using a web.

3.2. Population densities

Spider density estimates reported from field crops in various parts of Europe are compiled in Table 2. In cereal fields, spider densities of ≈ 2 –600 m⁻² were recorded (e.g., Topping and Sunderland, 1994a; Volkmar et al., 1994; Dinter and Poehling, 1995a; Toft et al., 1995), and single species, such as *E. atra* (Dinter, 1996) and *L. tenuis* (Sunderland, 1996; Topping and Sunderland, 1998) can reach densities of up to 27 and 62 m⁻², respectively. In a heavily-grazed pasture the peak density of *Oedothorax fuscus* was 155 m⁻² (De Keer and Maelfait, 1987) and that of *Erigone* species was 318 m⁻² (De Keer and Maelfait, 1988). Spider densities within the range of ≈ 10 –150 m⁻² were reported from sugar beet (Assmuth and Groh, 1984; Garbe and Heimbach, 1992). Somewhat lower numbers were found in maize (≈ 25 –90 m⁻²) and potato (≈ 10 –25 m⁻²) (Luczak, 1975; Nyffeler, 1982;

Table 1

Percentage of Linyphiidae individuals in the total spiders collected in various European field crops (arranged in order of decreasing percentage)

Habitat	Country	Collecting method	Linyphiidae (%)	Authors
Sugar beet	Germany	Pitfalls	99.8	Kleinhenz and Büchs (1993)
Beet	France	Pitfalls	99.6	Cocquempot (1988)
Garden lettuce	Germany	Pitfalls	99.5	Blick (1999)
Sugar beet	Germany	Eclector	99.2	Kleinhenz and Büchs (1993)
Wheat	Belgium	Pitfalls	99.0	Cottenie and De Clercq (1977)
Beans	France	Pitfalls	98.8	Cocquempot (1988)
Wheat	Germany	Pitfalls	98.4	Dinter (1995)
Peas	France	Pitfalls	98.0	Cocquempot (1988)
Maize	France	Pitfalls	97.6	Cocquempot (1988)
Potatoes	Germany	Pitfalls	96.5	Platen (1996)
Sugar beet	Germany	Eclector	96.0	Sokolowski (1995)
Wheat	Germany	D-vac	95.9	Dinter (1995)
Maize	Germany	Pitfalls	95.4	Beyer (1981)
Maize	Germany	Pitfalls	95.1	Samaké and Volkmar (2000)
Sugar beet	Germany	Pitfalls	95.0	Sokolowski (1995)
Sugar beet	Germany	Pitfalls	94.9	Beyer (1981)
Barley	Denmark	Pitfalls	94.1	Toft (1989)
Wheat	United Kingdom	D-vac	93.5	Topping and Sunderland (1994a)
Wheat	Germany	Eclector	93.2	Dinter (1995)
Wheat	Germany	Pitfalls	93.0	Basedow et al. (2000)
Rape	Germany	Pitfalls	92.2	Beyer (1981)
Wheat	France	Pitfalls	91.1	Cocquempot (1988)
Barley	Germany	Pitfalls	90.6	Volkmar (1996)
Sugar beet	Germany	Pitfalls	90.6	Samaké and Volkmar (2000)
Meadow (mown)	Switzerland	Pitfalls	90.0	Nyffeler (1982)
Rye	Germany	Pitfalls	88.9	Platen (1996)
Kohlrabi	Germany	Pitfalls	88.9	Beyer (1981)
Clover/grass	Germany	Pitfalls	86.4	Beyer (1981)
Wheat	Germany	Pitfalls	78.7	Beyer (1981)
Sugar beet	Poland	Pitfalls	73.1	Czajka and Goos (1976)
Wheat	Switzerland	Pitfalls	73.0	Nyffeler (1982)
Sugar beet	Czech Republic	Pitfalls	68.0	Luczak (1979)
Arable land	Switzerland	Pitfalls	62.4	Blick et al. (2000)
Alfalfa	Hungary	D-vac	51.7	Samu et al. (1996)
Alfalfa	Czech Republic	Pitfalls	51.0	Luczak (1979)
Wheat	Austria	Pitfalls	48.5	Thaler et al. (1977)
Rye	Poland	Sweeping	48.0	Luczak (1979)
Winter cereals	Finland	Sweeping	47.0	Huhta and Raatikainen (1974)
Alfalfa	Germany	Pitfalls, sweeping	44.1	Geiler (1963)
Wheat	Hungary	Pitfalls	35.4	Basedow et al. (2000)
Potato	Poland	Sweeping	34.6	Czajka and Kania (1976)
Alfalfa	Poland	Sweeping	32.0	Luczak (1979)
Potato	Poland	Sweeping	25.5	Luczak (1979)
Oats	Finland	Sweeping	14.5	Raatikainen and Huhta (1968)
Alfalfa	Hungary	Sweeping	5.9	Samu et al. (1996)
Alfalfa	Hungary	Pitfalls	1.6	Samu et al. (1996)
Overall mean \pm S.E.			74.9 \pm 4.2	

Table 2
Estimates of spider densities in European field crops (arranged according to crop type)^a

Crop	Country	Collecting method	Period (months)	Number of spiders (m ⁻²)	Authors
<i>Annual crops</i>					
Arable land	Germany	Quadrat	4–10	250	Heydemann (1962)
Wheat	United Kingdom	D-vac	3–8	10–120	Topping and Sunderland (1994a)
Wheat	United Kingdom	D-vac	4–8	5–300	Vickerman (1992)
Wheat	United Kingdom	D-vac	6–7	13–20	Moreby et al. (1994)
Wheat	United Kingdom	Quadrat + D-vac	5–7	3–20	Winder et al. (1994)
Wheat	United Kingdom	Multiple methods	5–8	11–36	Sunderland et al. (1987b)
Wheat	United Kingdom	Fenced pitfalls	4–7	10–146	Holland (1998)
Wheat	Holland	Fenced pitfalls	7	23–59	Jagers op Akkerhuis (1993)
Wheat	Germany	D-vac + eclector	7	38–567	Volkmar et al. (1994)
Wheat	Germany	D-vac	4–8	50–300	Dinter and Poehling (1995a)
Wheat	Germany	Flooding	5–7	10	Basedow (1998)
Wheat	Germany	Quadrat	7	54	Krause (1987)
Wheat	Switzerland	D-vac	5–7	10	Jmhasly and Nentwig (1995)
Wheat	Switzerland	Visual count	5–6	12–53	Nyffeler and Benz (1988a)
Wheat	Denmark	Distance method	6–7	100–450	Toft et al. (1995)
Barley	Denmark	Distance method	6–7	50–600	Toft et al. (1995)
Barley	United Kingdom	Multiple methods	5–6	61	Sunderland et al. (1987b)
Oats	Germany	Quadrat	7	32	Krause (1987)
Maize	Germany	Eclector	6	90	Lang (1998)
Maize	Germany	Quadrat	7	18	Krause (1987)
Maize	Switzerland	Visual count	6–7	13–35	Nyffeler (1982)
Maize	Belgium	Quadrat	7	26	Alderweireldt (1987)
Potato	Poland	Quadrat	8	24	Luczak (1975)
Sugar beet	Germany	Other	4–10	15–166	Assmuth and Groh (1984)
Sugar beet	Germany	Eclector	6–7	60–140	Garbe and Heimbach (1992)
Mean ± S.E.				91.6 ± 19.6	
<i>Perennial crops</i>					
Hay meadow	Switzerland	Visual count	6–7	13–25	Nyffeler and Benz (1988a)
Meadow	Poland	Soil cores	3–11	26–74	Kajak (1978)
Ryegrass	Belgium	Quadrat	7	43	Alderweireldt (1987)
Grass/cereal	United Kingdom	D-vac	1–12	5–60	Thomas and Jepson (1997)
Clover/grass	Ireland	D-vac	5–9	73	Curry and O'Neill (1978)
Alfalfa/grass	Sweden			70–131	Curry (1994)
Alfalfa	Hungary	Quadrat	6–9	21	Balogh and Loksa (1956)
Alfalfa	Hungary	D-vac	5–9	85	Samu et al. (1996)
Alfalfa	Hungary	D-vac	7–10	2–87	Samu et al. (1997)
Mean ± S.E.				52.1 ± 9.4	
Overall mean ± S.E.				81.2 ± 14.8	

^a In the case of a density range, the mean was calculated as (minimum value + maximum value)/2.

Alderweireldt, 1987; Lang, 1998). Densities in perennial gramineous and legume crops were similar to those recorded for annual row crops (Alderweireldt, 1987; Curry, 1994; Samu et al., 1996). Based on all these estimates, an overall mean value for the spider density of field crops of northern-temperate Europe of $\approx 80 \text{ m}^{-2}$ was computed (Table 2).

3.3. Prey selection

Feeding patterns of the numerically dominant spiders (linyphiids and lycosids) have been identified by means of visual observation in the field (Tables 3 and 4). The feeding patterns of linyphiids in various studies (encompassing wheat, maize and meadows in

Table 3

Percentage composition of prey types taken by linyphiid spiders in European gramineous crops

Crop	Country	Prey types ^a			
		Aphids	Collembola	Diptera	Others
Wheat	United Kingdom ^b	12.1	71.7	5.6	10.6
Wheat	Switzerland ^c	56.0	4.7	24.5	14.8
Wheat	Switzerland ^d	38.7	37.8	13.5	9.9
Maize	Switzerland ^d	50.0	34.6	7.7	7.7
Maize	Belgium ^e	56.7	35.8	3.0	4.5
Meadow (mown)	Switzerland ^d	27.9	48.7	7.8	15.6
Overall mean ± S.E.	All	40.2 ± 7.2	39.1 ± 8.9	10.4 ± 3.2	10.5 ± 1.7

^a Prey were collected from the webs of spiders (except for footnote b, where prey were collected from the chelicerae of spiders).

^b Sunderland et al. (1986a).

^c Jmhasly and Nentwig (1995).

^d Nyffeler and Benz (1988a).

^e Alderweireldt (1994).

Switzerland, UK, and Belgium) differ little (Table 3). Linyphiid webs are not located randomly in fields, but rather reflect the microdistribution of potential prey (Harwood et al., 2001a). The fragile, horizontal sheet webs of linyphiids, usually $\approx 1\text{--}74\text{ cm}^{-2}$ surface area (Sunderland et al., 1986a), may have evolved primarily for interception of small, soft-bodied insects, such as collembolans, dipterans, and aphids (Table 3); remains of larger and/or heavily-sclerotised prey (such as lepidopterans, heteropterans, and coleopterans) are rarely found in the webs of these spiders. However, some common linyphiids, such as *Oedothorax* species, appear to rely much less on use of a web (Thornhill, 1983), and species of the genus *Erigone* can capture prey outside the web (Alderweireldt, 1994). *E. atra*, under laboratory conditions, was observed to leave its web, chase, capture, and completely consume the fluid contents of a tiny staphylinid beetle (Aleochari-

nae) that was passing near the web on the ground (Sunderland, unpublished). It is likely that the true diet is wider than that inferred from prey remains in webs. DNA techniques, now undergoing rapid development for predation studies (Zaidi et al., 1999; Chen et al., 2000; Sunderland et al., 2002), hold promise for gaining a more comprehensive documentation of linyphiid diet. Lycosids are diurnal hunters and some species use a “sit-and-wait” foraging strategy (Ford, 1978; Stratton, 1985; Riechert, 1992). Lycosid individuals holding prey can be caught and preserved for later microscopical identification of spider and prey. In many cases the prey is too damaged to permit identification, but aphids, Collembola and Diptera have been identified (Nyffeler and Benz, 1988b). As far as is known, lycosids feed basically on the same prey groups as the linyphiids (high diet overlap) (Table 4). Individual spiders usually take more than one prey type. Such dietary mixing may be advantageous by optimising a balanced nutrient composition needed for survival and reproduction (Greenstone, 1979; Toft, 1995). The numerically dominant spiders in European crops appear to feed infrequently, since only 4–5% of the population are observed with food at any instant (Table 5), and this equates to approximately one prey killed per spider per day (see Section 5).

Table 4

Percentage composition of prey types taken by lycosid spiders (*Pardosa* spp.) in agricultural fields and woodland in eastern Switzerland (after Nyffeler and Benz, 1988b)^a

Prey type	Wheat	Meadow (mown)	Beech-spruce forest	Overall mean ± S.E.
Aphids	27.1	33.3	0.0	20.1 ± 10.2
Collembola	25.4	28.6	52.2	35.4 ± 8.4
Diptera	27.1	14.3	34.8	25.4 ± 6.0
Others	20.4	23.8	13.0	19.1 ± 3.2

^a Percentages deviate from values presented in the original publication because a large number of strongly masticated, unidentifiable prey items are not included here.

3.4. Spiders as predators of pests

Spider predation on aphids has been assessed using serological methods (Chiverton, 1987; Sopp and

Table 5

Percentage of spiders observed feeding: a comparison of studies in European and US agroecosystems

Crop	Geographical area	Number of spiders observed	Observation period ^a	Percentage of spiders feeding	Authors
Wheat ^b	Switzerland	2499	D	4.2	Nyffeler and Benz (1988b)
Meadow (mown) ^b	Switzerland	710	D	4.9	Nyffeler and Breene (1990)
Soybean ^c	Illinois	>79	D, N	12.0	LeSar and Unzicker (1978)
Cotton ^c	Mississippi	237	D	7.6	Young (1989)
Cotton ^b	Mississippi	3704	N	4.4	Hayes and Lockley (1990)
Cotton ^b	East Texas	308	D	4.0	Nyffeler et al. (1994a)
Cotton ^c	East Texas	1890	D, N	3.2	Nyffeler et al. (1987a)
Cotton ^c	Central Texas	2402	D	2.6	Nyffeler et al. (1992a)
Cranberry ^d	Massachusetts	7009	D	2.7	Bardwell and Averill (1997)
Vegetables ^d	Tennessee	2423	D	6.5	Riechert and Bishop (1990)
Overall mean ± S.E.				5.2 ± 0.9	

^a D: daytime, N: nighttime.^b Soil surface-dwellers.^c Foliage-dwellers.^d Soil surface-dwellers and foliage-dwellers.

Chiverton, 1987; Sunderland et al., 1987a; Janssens and De Clercq, 1990; Kennedy, 1990; Burn, 1992), and the findings have been verified and quantified through field and laboratory experiments (Sunderland et al., 1986a,b; Sunderland, 1987; Heidger and Nentwig, 1989; Sopp et al., 1992; Mansour and Heimbach, 1993; Jmhasly and Nentwig, 1995; Schröder et al., 1999). Foliage- and soil surface-dwelling spiders alike feed heavily on cereal aphids (i.e., *Metopolophium dirhodum*, *Rhopalosiphum padi*, and *Sitobion avenae*). The diet of linyphiids contains ≈10–60% of cereal aphids in winter wheat and maize (Nyffeler, 1982; Sunderland et al., 1986a; Alderweireldt, 1994). In these studies, the majority of aphids in the prey of the linyphiids were apterous and probably intercepted in spider webs after being knocked down from the foliage by wind and rain, or after dropping in response to the alarm pheromone produced by individuals attacked by predators (Bowers et al., 1972; Kislou and Edwards, 1972) or parasitoids (Gowling and Van Emden, 1994). According to Sunderland et al. (1986b), aphids in winter wheat dropped to the ground at a rate of 7.5–100 individuals m⁻² per day (increasing from late May to the first half of July). At low aphid densities early in the season there is a relatively greater proportion of aphids on the ground than later when the population has increased, and this is beneficial for pest control (Sopp et al., 1987). Apteræ are capable

of climbing back into the field layer (Winder, 1990) and are therefore still potentially harmful to the plants (Nyffeler and Benz, 1988a). However, reclimbing rate is negatively related to the abundance of generalist predators (including Linyphiidae) on the ground; 86% of aphids were calculated to reclimb in the absence of predators, compared to about 15% in wheat fields with average-density predator populations (Duffield et al., 1996). This principle of aphid control being facilitated by synergism between ground-based generalist predators and natural enemies foraging in the foliage has also been demonstrated by Losey and Denno (1999) in an aphid-ladybird-carabid system in alfalfa in the US. Spiders usually (Toft, 1995; Bilde and Toft, 1997; Beck and Toft, 2000), but not always (Kielty et al., 1999) prefer alternative foods (such as Collembola) to cereal aphids, and there is evidence from the field that fewer aphids are consumed when the availability of Collembola is high (Harwood et al., 2001b). This suggests that under diversified agricultural systems of the future, where more prey choice will be possible (Sunderland and Samu, 2000), the role of spiders in pest control may be reduced. However, there are other competing processes to consider, such as alternative foods enabling an early build up of spider populations in fields (Axelsen et al., 1997), early-instar aphids being unable to escape (and so dying) in linyphiid webs, even when they are not attacked by the spider (Sunderland et al., 1986b),

and “wasteful” or “superfluous” killing of pests by satiated spiders (Mansour and Heimbach, 1993; Samu and Bíró, 1993; Riechert and Maupin, 1998). On balance, it is likely that soil surface-dwelling spiders make a significant contribution to the control of cereal aphids, as is also suggested by the majority of manipulative field studies (Edwards et al., 1979; Sunderland et al., 1980; Chiverton, 1986; Gravesen and Toft, 1987; Winder, 1990; Burn, 1992; Lübke-Al Hussein and Triltsch, 1994; Holland and Thomas, 1997; Lang et al., 1999). Spider predation on agriculturally harmful aphids has also been recorded in meadows, oats, rape, potato, sugar beet, alfalfa, and sunflower (Dunn, 1949; Kajak, 1965; Foster, 1972; Suter and Keller, 1977; Nyffeler and Benz, 1979, 1981, 1982; Thornhill, 1983; Pekár, 2000). Many different species of pest aphids (including the key pests *Aphis fabae* and *Myzus persicae*) are captured and devoured by spiders. Significantly more root aphids (*Anoecia corni*) were recorded in parts of a meadow from which predators (mainly spiders and carabid beetles) had been excluded (Kajak, 1997).

Since small linyphiids feed largely on aphids and are able to build up fairly high numbers, they are suspected to play a useful role as natural control agents in damping aphid population explosions. Their efficiency as mortality agents of insect pests may be limited by their small size (usually $\approx 1\text{--}3$ mg fresh weight per individual) (Table 6), suggesting that they have a low individual prey killing capacity as a consequence of low food requirement. Indeed, the percentage of linyphiids feeding at any one time in the field was found to be low ($\approx 4\%$) (van Wingerden, 1977; Nyffeler and Benz, 1988a; Table 5). According

to an estimate by Nyffeler and Benz (1988a) based on feeding frequency, handling time, and diel activity period of the spider, a small linyphiid may kill, on the average, slightly less than one tiny prey item per day. By multiplying this value with the average spider density, it was estimated that small linyphiids in a winter wheat field near Zurich had killed perhaps, on average, ≈ 20 aphids m^{-2} per day in June. (At this time of the growing season, the numbers of aphids on the wheat plants reached $1000\text{--}5000$ m^{-2} .) Kennedy (1990), using ELISA to detect remains of *S. avenae* in linyphiids living in Irish cereal fields, calculated predation rates of $2.2\text{--}12.3$ m^{-2} per day (varying seasonally) and reductions in peak aphid populations of $4.1\text{--}37.0\%$ (varying annually). Sunderland et al. (1986b) estimated that ≈ 30 aphids m^{-2} per day were killed by linyphiids in winter wheat in the UK, and Fraser (1982) calculated that linyphiids reduced the peak population of *S. avenae* in a field of winter wheat by 37%. In a re-analysis of the data of Fraser (1982), it was estimated that linyphiids reduced peak aphid populations by 49% (Chambers and Aikman, 1988). Winder et al. (1994) calculated that polyphagous predators caused reductions of 0.7 to $>50\%$ of populations of this aphid (varying according to season and year), and that linyphiids made a small but consistent contribution to this overall effect. In general, the data suggest that linyphiids make a useful contribution to cereal aphid control (especially, if mortality due to wasteful killing and death in webs were added to the above figures), but would not be sufficient, by themselves, to prevent aphids causing yield loss.

Apart from aphids, dipterans are a major food source for many spider species (Kajak, 1965;

Table 6
Weight (mean fresh weight per individual) of linyphiid spiders in European field crops

Spider taxa	Sample size	Mean fresh weight (mg) ^a	Authors
Linyphiidae	120	1.04	Basedow et al. (1991)
Linyphiidae	Not given	1.11	Luczak (1975)
Linyphiidae	14	1.40	Nyffeler and Benz (1988a)
Linyphiidae	Not given	2.50	Heydemann (1962)
<i>E. atra</i> male	17	1.53	Dinter and Poehling (1995b)
<i>E. atra</i> female	19	3.76	Dinter and Poehling (1995b)
<i>O. apicatus</i> male	20	1.11	Dinter and Poehling (1995b)
<i>O. apicatus</i> female	19	5.57	Dinter and Poehling (1995b)
Overall mean \pm S.E.		2.25 ± 0.58	

^a Fresh weight calculated as four times dry weight, assuming an average spider water content of 75% (Pulz, 1987).

Nyffeler, 1982, 1999). Spiders have been reported to feed on the frit fly (*Oscinella frit*), hessian fly (*Mayetiola destructor*), and wheat blossom midges (*Contarinia tritici*, *Sitodiplosis mosellana*), all of which are key pests in European cereal fields (Basedow, 1973; Sunderland, 1987; Heidger and Nentwig, 1989). Using predator exclusion techniques, Holland et al. (1996) recorded no effect of polyphagous predators (including spiders) on *S. mosellana* populations in wheat, but Basedow (1975) found that midge predation was reduced by 84% when ground-dwelling predators were excluded. In addition to their direct effects on pest populations, spiders can also exert an influence as one component of an assemblage of natural enemies (Sunderland et al., 1997; Sunderland, 1999), where the interactions between spiders and other natural enemies can have either positive or negative effects on pest control, depending on crop and season (see also Section 4.4). Generalist predator assemblages (which frequently included spiders) were found to reduce pest numbers significantly in 79% of the 52 studies reviewed by Symondson et al. (2002).

Usually spiders eat larvae or adults of insects; feeding on insect eggs has been observed, to date, only in captivity with regard to European studies (Jones-Walters, 1993).

4. Spiders in US field crops

4.1. Taxonomic composition

More than 600 spider species (44% web-builders, 56% hunters) are associated with US field crops (Young and Edwards, 1990). Web-building spiders are represented mainly by the families Tetragnathidae, Araneidae, Linyphiidae, Theridiidae, and Dictynidae; the hunters by Oxyopidae, Salticidae, Clubionidae, Thomisidae, and Lycosidae (Nyffeler, 1999). Spider guild structure is more complex compared to Europe (Table 7) and there is considerable variation from crop to crop and region to region (Uetz et al., 1999). Representatives of the family Linyphiidae are less common in the US (usually <25% of total spider individuals) (Table 7). Schmaedick and Shelton (2000), however, found the arachnofauna on the foliage of cabbage in New York state to be >70% Linyphiidae. Orb-weavers (e.g. *Tetragnatha laboriosa*) are fairly

common in some locations (Table 7) (LeSar and Unzicker, 1978; Culin and Yeagan, 1982). Hunters make up >50% of the spider individuals collected in US fields in most studies (Table 7). Among them, *Oxyopes salticus* (Oxyopidae) is a particularly prominent agroecosystem coloniser in the US (Dean and Sterling, 1987; Young and Edwards, 1990). This species is often the commonest spider predator in cotton and soybean throughout extensive growing areas from the southeast (North Carolina, South Carolina, Georgia, Alabama, and Mississippi) to the southwest (Arkansas, Louisiana, and Texas) (Young and Lockley, 1985). West of the 100th degree of longitude the climate is much drier, and Oxyopidae as a dominant family is replaced there by the Thomisidae. Accordingly the spider fauna in regions such as west Texas and Arizona is dominated by thomisid spiders (e.g., *Misumenops* spp.) (Plagens, 1983; Dean and Sterling, 1987). A spider fauna that differs somewhat from the rest of the country is found on the Californian west coast, where the lycosid *Pardosa ramulosa* is often the commonest spider inhabitant of crop fields (Yeagan and Dondale, 1974; Orazé et al., 1988).

Spider individuals of small body size (including high percentages of immatures) numerically dominate the spider fauna in US field crops (Young and Edwards, 1990). For instance, the average body length of *O. salticus* was found to be in the range of 4–5 mm in cotton growing areas of Mississippi and Texas (Lockley and Young, 1987; Nyffeler et al., 1994a).

4.2. Population densities

Thorough assessments of spider densities have been conducted in the US, especially in cotton and soybean. This is probably attributable to the fact that great efforts have been undertaken by entomologists to monitor pests and predators in these two crops, which are of major economic importance. During an extensive survey throughout Texas, Dean and Sterling (1987) recorded spider numbers in unsprayed cotton fields (with a vacuum insect net; D-vac) at between 0.2 (south Texas) and 2.3 individuals per m of row (east Texas). The overall mean throughout Texas (including data not shown in Table 8) is 0.8 spiders per m of row, which equates to ≈ 0.8 spiders m^{-2} (based on a row spacing of approximately 1 m). Density assessments on cotton in Arkansas, Louisiana,

Table 7

Percentage contribution of three major spider groups to the arachnofauna of US field crops (arranged according to crop type)^a

Crop	State	Collecting method	Percentage			Authors
			Linyphiidae	Orb-weavers	Hunters	
<i>Annuals</i>						
Wheat	OK	D	29.6	47.5	16.6	Greenstone (2001)
Wheat	CO	D	23.0	19.0	42.0	Greenstone (2001)
Wheat	Canada	P	3.4	0.0	84.2	Doane and Dondale (1979)
Sorghum	OK	P	39.0	1.1	43.0	Bailey and Chada (1968)
Rice	TX	P, S	22.5	6.9	70.6	Woods and Harrel (1976)
Rice	CA	D	19.3	<1.8	78.9	Oraze et al. (1988)
Rice	CA	St	5.1	<1.1	93.8	Oraze et al. (1988)
Rice	AR	S	7.3	24.2	68.0	Heiss and Meisch (1985)
Soybean	KY	P	46.8	0.6	15.6	Culin and Yeargan (1983b)
Soybean	KY	Sk	0.9	32.0	20.2	Culin and Yeargan (1983a)
Soybean	OH	V	43.0	44.0	<13.0	Balfour and Rypstra (1998)
Soybean	VA	P	13.1	0.3	86.2	Ferguson et al. (1984)
Peanut	TX	V	3.1	2.0	88.7	Agnew and Smith (1989)
Peanut	TX	P	1.8	<1.7	95.7	Agnew and Smith (1989)
Cotton	TX	D, P, V	12.0	11.0	68.8	Dean et al. (1982)
Cotton	TX	D	1.9	9.4	81.8	Dean et al. (1988)
Cotton	AR	V, O	10.4	13.9	69.0	Whitcomb et al. (1963b)
Vegetables	TN	V	23.8	16.6	36.2	Riechert and Bishop (1990)
Mean ± S.E.			17.0 ± 3.5	12.9 ± 3.6	59.6 ± 6.9	
<i>Perennials</i>						
Alfalfa	VA	D	48.6	38.3	12.5	Howell and Pienkowski (1971)
Alfalfa	VA	S	2.4	56.8	40.3	Howell and Pienkowski (1971)
Alfalfa	KY	P	42.7	2.8	21.7	Culin and Yeargan (1983b)
Alfalfa	KY	D	8.6	50.6	14.8	Culin and Yeargan (1983a)
Alfalfa	CA	D	33.6	1.3	63.0	Yeargan and Dondale (1974)
Grassland	AR	P	15.2	0.8	82.7	Whitcomb et al. (1963a)
Grassland	TX	D	2.4	33.0	61.0	Dean et al. (1988)
Grassland	TX	S	0.7	9.6	89.2	Dean et al. (1988)
Cranberry	MA	V, S	4.2	34.6	61.2	Bardwell and Averill (1997)
Blueberry	ME	P	1.0	0.1	95.3	Collins et al. (1996)
Mean ± S.E.			15.9 ± 5.9	22.8 ± 7.0	54.2 ± 9.7	
Overall mean ± S.E.			16.6 ± 3.0	16.5 ± 3.4	57.6 ± 5.5	

^a D: D-vac; P: pitfall; V: visual search; S: sweeping; Sk: shake cloth; St: sticky trap; O: others.

Mississippi, Oklahoma, Arizona, and California yielded similar values to Texas (Whitcomb et al., 1963b; Johnson et al., 1976; Gonzalez et al., 1977; Smith and Stadelbacher, 1978; Stam et al., 1978; Plagens, 1983). Deitz et al. (1976) found values ranging from 0.4 to 3.2 spiders m⁻² (overall mean ≈ 1.4 spiders m⁻²) in unsprayed soybean fields in North Carolina. Values of the same order of magnitude were reported from soybean in Kentucky and peanut in Texas (Agnew and Smith, 1989; Anderson

and Yeargan, 1998). A mean spider density of 0.7 m⁻² was recorded in unsprayed winter wheat in Colorado, and of 2.7 m⁻² in winter wheat in Oklahoma (Greenstone, 2001). Based on an extensive literature survey, taking into account unsprayed and sprayed fields, an overall mean spider density of ≈ 2 m⁻² was computed for annual row crops in the US (Table 8). Where fields are heavily sprayed, extremely low spider densities (0.02–0.1 m⁻²) have been reported (Skinner, 1974; W.L. Sterling, pers. comm.). Much

Table 8
Estimates of spider density in US field crops (arranged by crop type)^{a,b}

Crop	Location	Collecting method	Period (months)	Number of spiders (m ⁻²)	Authors	
<i>Annuals</i>						
Cotton	Alabama	Not known	Not known	0.02–0.1	Skinner (1974)	
	Arizona	Ground cloth	6–9	1.3–2.3	Plagens (1983)	
	Arkansas	Plant examination	6–10	0.8	Whitcomb et al. (1963b)	
	California	Plant examination	6–9	0.8	Gonzalez et al. (1977)	
	Louisiana	D-vac	6–7	0.6–0.8	Stam et al. (1978)	
	Mississippi	D-vac	6–8	0.1	Dinkins et al. (1970)	
	Oklahoma	Plant examination	6–8	1.5–2.5	Johnson et al. (1976)	
	Texas (central)	D-vac	5–9	1.0	Dean and Sterling (1987)	
	Texas (east)	D-vac	5–9	2.3	Dean and Sterling (1987)	
	Texas (north)	D-vac	5–9	0.8	Dean and Sterling (1987)	
	Texas (south)	D-vac	5–9	0.2	Dean and Sterling (1987)	
	Texas (west)	D-vac	5–9	0.4	Dean and Sterling (1987)	
	Soybean	Kentucky (narrow rows)	Beat sheet	7–8	2.4–3.7	Anderson and Yeargan (1998)
		Kentucky (wide rows)	Beat sheet	7–8	1.4–2.3	Anderson and Yeargan (1998)
Kentucky		Shake cloth	4–12	1–14	Culin and Yeargan (1983a)	
Louisiana		Plant examination	7–10	0.04–0.05	Fuller and Reagan (1988)	
North Carolina (east)		Ground cloth	7–9	0.4–1.8	Deitz et al. (1976)	
North Carolina (west)		Ground cloth	7–9	0.4–3.2	Deitz et al. (1976)	
Ohio		Quadrat	5–12	8	Halaj et al. (2000)	
Sorghum	Louisiana	Plant examination	7–10	0.02–0.04	Fuller and Reagan (1988)	
Vegetables	Tennessee	Quadrat	Not given	1–8	Riechert (1990)	
Wheat	Colorado	D-vac + ground search	10–6	0.5–10	Greenstone (2001)	
	Oklahoma	D-vac + ground search	Spring	2.7	Greenstone (2001)	
Mean ± S.E.				1.99 ± 0.44		
<i>Perennials</i>						
Alfalfa	California	D-vac + echo sampler	5–8	15–145	Summers et al. (1984)	
Alfalfa	California	D-vac	1–12	1–60	Yeargan and Cothran (1974)	
Alfalfa	Virginia	D-vac	1–12	1–31	Howell and Pienkowski (1971)	
Alfalfa	Kentucky	D-vac	4–12	2–122	Culin and Yeargan (1983a)	
Meadow	Ontario	Quick trap + suction	4–10	30–77	Dondale (1971)	
Meadow	New York	Not known	Not known	51	Wolcott (1937) ^c	
Meadow ^d	Tennessee	Quick trap + suction	4–12	56	Van Hook (1971)	
Meadow	Texas	D-vac	7–9	6–10	Nyffeler et al. (1987a)	
Mean ± S.E.				44.6 ± 8.6		
Overall mean ± S.E.				12.3 ± 3.8		

^a In the case of a density range, the mean was calculated as (minimum value + maximum value)/2.

^b Dinkins et al. (1970), Stam et al. (1978), Culin and Yeargan (1983a) and Dean and Sterling (1987) presented their data as “numbers per meter of row”; we converted these values to “number of spiders per square meter” assuming approximately 1 m row spacing (as is the case in Texas; W.L. Sterling, pers. comm.). In the study of Anderson and Yeargan (1998), row spacing was 0.46 m (narrow) and 0.92 m (wide), and hence their values were adjusted using a correction factor of ×2.2 and ×1.1, respectively.

^c Cited in Dondale (1971).

^d Old field.

higher densities are found in perennial row crops (e.g. alfalfa) and meadows, giving an overall mean density of $\approx 45 \text{ m}^{-2}$ (Table 8). In perennial row crops hunters and orb-weavers, rather than Linyphiidae, predominate (Table 7).

4.3. Prey selection

The feeding patterns of spiders in US field crops, based on 10 different studies in soybean, cotton, peanut, alfalfa and vegetables, are presented in

Table 9
Percentages of seven major prey types in the diet of spiders in US field crops

Study ^a	Percentage						
	Heteroptera	Homoptera	Coleoptera	Diptera	Hymenoptera	Araneae	Lepidoptera
1	17.7	36.6	0.0	40.5	3.8	0.0	0.0
2	3.1	25.2	38.5	18.5	5.1	0.0	5.1
3	5.8	4.4	50.4	13.1	1.5	4.4	8.0
4	54.2	16.7	0.0	18.8	0.0	0.0	6.2
5	31.0	15.5	22.4	12.1	1.7	15.5	1.7
6	27.7	9.6	5.3	13.8	22.3	17.0	0.0
7	1.0	43.6	7.9	11.4	31.9	1.4	0.6
8	32.7	7.3	3.2	6.4	9.5	17.3	17.3
9	13.4	13.4	45.2	19.1	0.0	0.0	8.9
10	11.5	24.1	6.0	22.1	0.6	19.6	1.2
Overall mean \pm S.E.	19.8 \pm 5.2	19.6 \pm 4.0	17.9 \pm 6.2	17.6 \pm 2.9	7.6 \pm 3.4	7.5 \pm 2.7	4.9 \pm 1.7

^a 1: LeSar and Unzicker (1978), Tetragnathidae, soybean, Illinois; 2: Culin and Yeorgan (1982), Araneidae and Tetragnathidae, soybean, Kentucky; 3: Hayes and Lockley (1990), Lycosidae, cotton, Mississippi; 4: Lockley and Young (1987), Oxyopidae, cotton, Mississippi; 5: Young (1989), Salticidae, cotton, Mississippi; 6: Nyffeler et al. (1992a), Oxyopidae, cotton, central Texas; 7: Nyffeler and Sterling (1994), spider assemblage, cotton, east Texas; 8: Agnew and Smith (1989), spider assemblage, peanut, west Texas; 9: Riechert and Bishop (1990), spider assemblage, vegetables, Tennessee; 10: Yeorgan (1975a), Lycosidae, alfalfa, California.

Table 9. Overall, the diet of agroecosystem spiders in the US is more diverse than in Europe (cf. Tables 3 and 4). Heteroptera, Homoptera, Coleoptera, Diptera, Hymenoptera, and Lepidoptera are the insects most frequently recorded as spider prey (Table 9). In addition, spiders were observed feeding on other spiders (a behaviour typical of hunting spiders). Seven prey taxa (Table 9) comprise 95% of total prey consumed. The high overall mean percentage of Coleoptera in the diet is probably due to two studies (2 and 3 in Table 9) referring to larger spider species that occur in field crops in low numbers (i.e. *Neoscona arabesca* and large Lycosidae), and whose contribution to the spiders' overall predation impact can be considered minor (Nyffeler, unpublished). The vast majority of agroecosystem spiders, however, are small individuals (e.g. *O. salticus*) that usually cannot pierce the strongly-sclerotised coleopteran integument, and the overall impact of spider predation on coleopterans in US field crops is probably rather small (Nyffeler et al., 1994a).

As in Europe, agroecosystem spiders feed mostly on tiny prey (<4 mm long) (LeSar and Unzicker, 1978; Young and Edwards, 1990; Nyffeler et al., 1994a), and a low percentage are feeding at any one moment in the field (Table 5).

4.4. Spiders as predators of pests

Using a radiolabelling technique spiders were shown to feed on lepidopteran pests (eggs and/or larvae of the tobacco budworm, bollworm, and cotton leafworm) in cotton fields in Texas (McDaniel and Sterling, 1979, 1982; McDaniel et al., 1981; Gravina and Sterling, 1983; Nuessly and Sterling, 1994). The spiders involved were mainly hunters from the families Oxyopidae, Salticidae, Thomisidae, and Clubionidae. These findings were verified by ELISA studies, cage experiments, and visual observations (Whitcomb et al., 1963b; Whitcomb and Bell, 1964; Whitcomb and Eason, 1967; Whitcomb, 1967a,b; Lingren et al., 1968; Ruberson and Greenstone, 1998).

In soybean fields in Florida and South Carolina radiolabelling and visual observation have shown that spiders eat various stages of *Anticarsia gemmatalis* and other noctuid caterpillars (Buschman et al., 1977; McCarty et al., 1980; Godfrey et al., 1989; Gregory et al., 1989). Representatives of the families Oxyopidae, Salticidae, Thomisidae, and Clubionidae are known to be the main spider predators of lepidopteran pests in this crop (Buschman et al., 1977; Richman et al., 1980; Elvin et al., 1983; Reed et al., 1984; Gregory et al., 1989). Noctuid damage to maize, by *Pseudaletia unipuncta*, was significantly increased in

plots where predators (including Lycosidae, Linyphiidae, Thomisidae) were experimentally removed (Clark et al., 1994). The density of *Hemileuca oliviae*, a pest of forage grasses, was increased significantly by removing predators, including Araneidae (Shaw et al., 1987). Similar reductions of caterpillar pests by predator assemblages containing spiders have been demonstrated in brassica crops (Schmaedick and Shelton, 1999), sorghum and sugarcane (Fuller and Reagan, 1988). Radiolabelling has shown that spiders consumed cotton fleahopper *Pseudatomoscelis seriatus* (Heteroptera: Miridae) (Breene and Sterling, 1988; Breene et al., 1988–1990). The spiders involved were mainly Oxyopidae, Salticidae, and Thomisidae, as was also verified by visual observations in the field (Dean et al., 1987; Nyffeler et al., 1987b, 1992a,b). ELISA has revealed that spiders (especially Oxyopidae and Salticidae) eat the stink bug *Nezara viridula* (Heteroptera: Pentatomidae) in soybean fields in Louisiana (Ragsdale et al., 1981). These spiders are not deterred by the repugnant odour produced by stink bugs as a defence (Nyffeler et al., 1994a). They also feed heavily on *Lygus lineolaris*, a key pest in Mississippi cotton (Young and Lockley, 1986; Lockley and Young, 1987; Young, 1989). Thomisids and other spiders were observed to prey on pest mirids (*Labops hesperius* and *Irbisia brachycera*) and leafhoppers in Utah grassland (Araya and Haws, 1991).

From all these studies, it is clear that spiders often prey on lepidopteran and heteropteran pests and on various aphids, leafhoppers, treehoppers, and plant hoppers, which are potentially harmful by draining nutrients from plants and/or as vectors of plant diseases (Wheeler, 1973; LeSar and Unzicker, 1978; Culin and Yeargan, 1982; Orazé and Grigarick, 1989; Letourneau, 1990; Bardwell and Averill, 1997). Russian wheat aphid (*Diuraphis noxia*) densities were up to 11 times higher in wheat plots from which natural enemies (including Tetragnathidae and Thomisidae) had been excluded (Mohamed et al., 2000). In a study conducted in Texas cotton, the percentage of aphids in the diet of *O. salticus* was low compared with the percentage of aphids in the pool of potential prey (Nyffeler et al., 1987a). This suggests that aphids had been avoided by the spiders as a prey. Possibly, aphids are a low quality prey for lynx spiders, as for wolf spiders (Toft, 1995).

Hunting spiders are considered to be of particular importance as predators of the various stages of crop pests (Muniappan and Chada, 1970a; Horner, 1972; Young and Lockley, 1986; Lockley and Young, 1987; Young, 1989). They are mobile foragers that actively patrol the plant surface in search of larvae and adults of lepidopterans and heteropterans (Whitcomb, 1974). Lycosidae were often seen attacking tethered larvae of lepidopterous pests in maize (Brust et al., 1986). Various techniques have shown that even insect eggs are devoured by hunting spiders (Nyffeler et al., 1990). Some spiders, such as *Cheiracanthium mildei*, are also able to attack leaf-mining lepidopteran larvae through the lower epidermis of the leaf (Corrigan and Bennett, 1987). Occasionally spiders in US field crops feed on pests from other insect orders, including coleopterans, but this seems to be of little consequence economically (Yeagan, 1975a; LeSar and Unzicker, 1978; Culin and Yeargan, 1982; Young and Lockley, 1985; Hudson et al., 1988; Hough-Goldstein et al., 1993; Bardwell and Averill, 1997). Predation by lynx spiders on small larvae of *Leptinotarsa decemlineata* has been observed in the field, and the impact of spiders on the population dynamics of this pest may have been underestimated (Hilbeck and Kennedy, 1996).

Direct predation is not the only mechanism whereby predators affect crop protection. Spiders (*Pisurina mira*) that had their chelicerae glued together caused nearly as much grasshopper mortality and grass yield increase as did unmanipulated spiders (Schmitz et al., 1997). The mere presence of predators can induce behavioural and physical changes in herbivores (e.g. shifts in activity periods, diet and growth rate; Stamp, 1997). Presence of *Hogna helluo*, for example, caused reduction in feeding by *Diabrotica undecimpunctata howardi* and reduced damage to host plants (Snyder and Wise, 2000).

Apart from pests, spiders also feed on other predators and on parasitoids (Whitcomb, 1974; Randall, 1982; Willey and Adler, 1989; Araya and Haws, 1991; Nyffeler et al., 1994a,b; Fagan et al., 1998; Hodge, 1999). The phenomenon of mutual predation within the same trophic level is known as 'intraguild predation' (Polis and McCormick, 1987; Rosenheim, 1998; Wise and Chen, 1999; Brodeur and Rosenheim, 2000). Short of actual predation, one group of predators can also affect another by triggering behaviours, such as emigration from the field, that avoid intraguild

Table 10
Estimated percentage of predators in the diets of spiders in Europe and the US^a

Location	Crop	Spiders	Percentage	Authors
<i>Europe</i>				
Switzerland	Wheat	Linyphiidae	<10	Nyffeler and Benz (1988a)
United Kingdom	Wheat	Linyphiidae	<10	Sunderland et al. (1986a)
Switzerland	Wheat	Web-weavers	<10	Jmhasly and Nentwig (1995)
Switzerland	Wheat	Orb-weavers	<10	Nyffeler and Benz (1979)
Switzerland	Barley	Orb-weavers	<10	Nyffeler and Benz (1979)
Switzerland	Oats	Orb-weavers	<10	Nyffeler and Benz (1979)
Switzerland	Rye	Orb-weavers	<10	Nyffeler and Benz (1979)
Switzerland	Maize	Orb-weavers	<10	Nyffeler and Benz (1979)
Belgium	Maize	Linyphiidae	<10	Alderweireldt (1994)
Switzerland	Rape	Orb-weavers	<10	Nyffeler and Benz (1979)
<i>United States</i>				
Kentucky	Soybean	Orb-weavers	≈25	Culin and Yeargan (1982)
Illinois	Soybean	Orb-weavers	≈10	LeSar and Unzicker (1978)
Mississippi	Cotton	Oxyopidae	≈10	Lockley and Young (1987)
Texas (east)	Cotton	Oxyopidae	≈30–40	Nyffeler et al. (1987a,b)
Texas (central)	Cotton	Oxyopidae	≈30–40	Nyffeler et al. (1992a)
Mississippi	Cotton	Salticidae	≈20	Young (1989)
Mississippi	Cotton	Lycosidae	≈20	Hayes and Lockley (1990)
Texas (east)	Cotton	Orb-weavers	<10	Nyffeler et al. (1989)
Texas (east)	Cotton	Theridiidae	≈75	Nyffeler et al. (1988)
Texas	Peanut	Hunting spiders	≈50	Agnew and Smith (1989)
California	Alfalfa	Lycosidae	≈30	Yeargan (1975a)

^a “Orb-weavers” refers to Tetragnathidae or Araneidae or both (depending on study), “web-weavers” refers to Linyphiidae, Araneidae, Tetragnathidae, Theridiidae and Agelenidae, “hunting spiders” refers to Oxyopidae, Lycosidae and Thomisidae.

predation (Moran and Hurd, 1994). Predaceous arthropods can make up a substantial percentage of the spiders’ diet, especially in spider communities dominated by hunting spiders (e.g., Lycosidae, Oxyopidae, and Salticidae) in crop fields of the southern US (Table 10). The question has been raised, whether the habit of certain spiders to feed heavily on each other, and on other predators, reduces their value in biological control (Hodge, 1999). A recent experimental study by Snyder and Wise (2001), conducted in gardens of spring cucumber and summer squash in Kentucky, provides evidence that spiders may indeed exert an indirect negative effect on pest control through intraguild predation on other predators. Although lycosid spiders caused fruit production to increase by feeding on important early-season herbivores in spring cucumber gardens, they strongly reduced squash yield by feeding on other predators in summer squash gardens, thereby weakening the ability of predators to control late-season herbivores.

5. Discussion

5.1. Taxonomic composition

A comparison of the spider faunas in field crops of Europe and the US shows that there are significant differences. A single spider guild, made up of small linyphiids only, strongly dominates throughout large parts of Europe. The spider fauna of European field crops is very uniform, which contrasts with the situation in US field crops. The arachnofauna in the US is more evenly dispersed over families, and hunting spiders from various families make up a large percentage (Young and Edwards, 1990; Greenstone, 2001). Thus the ratio ‘web-builders/hunters’, which could be an indicator of community function, differs considerably between the two continents.

Bristowe (1939) noted that spider faunas can differ between geographic regions (especially along a north–south axis), and that this is governed

primarily by climate. In Europe, there may be a trend of progressive reduction in the proportion of Linyphiidae moving along the west–east axis (Table 1), but the major changes are related to latitude. Europe and the US are of comparable area (both approximately 10 million km²); Europe stretches from 71° to 30°, and the US (excluding Alaska and Hawaii) from 49° to 25° northern latitude. Agroecosystem spiders have been investigated mainly between 60° and 47° in Europe, but between 45° and 29° in the US (Table 11). Thus, the agricultural landscapes investigated in the US occur in distinctly more southern regions (latitudinal difference = 15° – 18°), encompassing the subtropical climate of Florida, Louisiana, Mississippi, and most of Texas, the dry desert or semi-arid steppe climates of west Texas, New Mexico, Arizona, and southeast California, as well as the Mediterranean climate of most of California. The overall mean annual temperature of the European study areas is ≈9°C, compared to ≈15°C in the US (Table 11). It is interesting to compare the data on spider composition from the southern US with data from South America, located even closer to the equator. In studies conducted near Lima, Peru (12°S latitude, mean annual temperature of 19°C), it was found that 80–90% of the spiders collected from cotton were hunting spiders (predominantly Anyphaenidae, Clubionidae, Salticidae and Thomisidae), whereas Linyphiidae constituted only 1% (Aguilar, 1977, 1979). Thus hunting spiders dominate in Peru, just as in the southern US.

Bristowe (1939) discovered that the percentage of Linyphiidae in the total spider fauna increases from the equator towards higher latitudes, while the percentage of Salticidae decreases. This rule applies not only to Europe, but also to North America (Enders, 1975; Gertsch, 1979). The difference between Europe and the US in the relative abundance of linyphiids is also reflected in the taxonomic composition of spiders ballooning above agricultural landscapes. The proportion of linyphiids in the aerial spider fauna is 2.5 times higher in European studies than in those from the US (85% vs. 34%) (Table 12). Thomas and Jepson (1999) suggested that there is a correlation between the relative abundance of linyphiids in the air and on the ground. Ballooning is the major mode by which agroecosystems are colonised by spiders (Bishop and Riechert, 1990; Weyman, 1993; Thorbek et al., 2002; Weyman et al., 2002). The observation that linyphiids

Table 11

Comparison of mean annual temperatures in relation to latitude, for locations in Europe and the US where the ecology of spiders in agroecosystems has been investigated

	Latitude (°)	Temperature (°C)
<i>Europe</i>		
Turku, Finland	60.5	4.7
Copenhagen, Denmark	55.7	7.8
Kiel, Germany	54.3	7.7
Dublin, Ireland	53.4	9.3
Berlin, Germany	52.5	8.9
Hannover, Germany	52.5	8.9
Braunschweig, Germany	52.3	9.3
Warsaw, Poland	52.2	7.5
Göttingen, Germany	51.6	9.2
Leipzig, Germany	51.4	8.5
London, United Kingdom	51.2	9.6
Antwerp, Belgium	51.2	10.3
Dresden, Germany	51.1	9.1
Halle, Germany	51.0	8.1
Giessen, Germany	50.6	9.6
Prague, Czech Republic	50.1	9.2
Darmstadt, Germany	49.9	9.8
Paris, France	49.0	11.2
Munich, Germany	48.1	7.7
Basel, Switzerland	47.6	8.9
Budapest, Hungary	47.5	10.9
Zurich, Switzerland	47.4	8.7
Innsbruck, Austria	47.3	8.8
Overall mean ± S.E.		8.9 ± 0.3
<i>US</i>		
Geneva, NY	42.9	8.7
Amherst, MA	42.4	8.6
Ames, IA	42.0	9.1
Urbana, IL	40.1	10.9
Newark, DE	39.7	12.5
Cincinnati, OH	39.0	12.2
Davis, CA	38.5	15.9
Lamar, CO	38.1	11.8
Lexington, KY	38.0	12.7
Blacksburg, VA	37.2	11.2
Fayetteville, AR	36.1	14.1
Stillwater, OK	36.1	15.3
Knoxville, TN	35.9	15.0
Raleigh, NC	35.9	15.7
Clemson, SC	34.7	15.9
Stoneville, MS	33.4	17.1
Auburn, AL	32.6	17.1
Abilene, TX	32.4	17.9
Las Cruces, NM	32.3	16.0
Tucson, AZ	32.1	20.2
Tifton, GA	31.5	18.7
College Station, TX	30.6	19.8
Baton Rouge, LA	30.5	19.9
Gainesville, FL	29.7	20.2
Overall mean ± S.E.		14.9 ± 0.7

Table 12

The percentage of Linyphiidae in the aerial spider fauna (ballooning aeronauts) of Europe and the US

	Percentage	Authors
<i>Europe</i>		
United Kingdom	97.0	Sunderland (1991)
United Kingdom	96.0	Smith (1904)
United Kingdom	92–96	Thorbek et al. (2002)
The Netherlands	95.2	Meijer (1977)
United Kingdom	>95.0	Thomas and Jepson (1999)
United Kingdom	93.8	Bristowe (1939)
United Kingdom	91.1	Duffey (1963)
United Kingdom	81.3	Hardy (cited in Bristowe, 1939)
Denmark	77.0	Nielsen (1932)
Switzerland	68.8	Blandenier and Fürst (1998)
Germany	64.0	Barthel (1997)
United Kingdom	63.0	Freeman (1946)
Overall mean \pm S.E. 84.7 \pm 3.82		
<i>US</i>		
California	59.5	Yeargan (1975b)
Washington	56.8	Crawford et al. (1995)
Missouri	44.9	Greenstone et al. (1987)
Texas	42.0	Dean and Sterling (1985)
Texas	31.2	Salmon and Horner (1977)
Tennessee	20.8	Bishop and Riechert (1990)
Texas	20.4	Agnew and Smith (1989)
Florida	19.0	Plagens (1986)
Washington	8.4	Crawford and Edwards (1986)
Overall mean \pm S.E. 33.7 \pm 6.01		

are dominant in European study areas, located at higher northern latitudes, whereas hunting spiders are in general more prominent in US study areas, located at lower latitudes, fits the pattern described by Bristowe (1939). Why is this the case? Five hypotheses, that are not necessarily mutually exclusive, are discussed below:

- (1) Salticidae, Oxyopidae, and some other hunter families show a preference for warmer regions. After comparing spiders in different temperate and tropical habitats, and analysing differences in life cycles, Jocqué (1984) hypothesised that the distribution of many hunting spiders is limited to warmer regions, because at low temperatures they lose speed and hunting efficiency. This may explain why Salticidae and Oxyopidae are missing from crop fields in parts of Europe. In the western, central, and Scandinavian parts of Europe, oxyopids occur in non-crop habitats only, and

are generally very rare (Bellmann, 1997). This changes in the warmer, Mediterranean regions of southern Europe (Greece, Spain, Portugal, etc.) (Bristowe, 1939). Near Evora, Portugal, it has been observed that Salticidae and Oxyopidae constitute a high percentage ($\approx 40\%$) of the spider fauna of a vineyard ecosystem, whereas the Linyphiidae are correspondingly less ($\approx 6\text{--}28\%$) (Nobre and Meierrose, 2000; Nobre et al., 2000). Evora is located at 38°N latitude and has a mean annual temperature of 16°C , which is about equal to the temperature in areas of the subtropical and Mediterranean regions of the US (Table 11).

- (2) Linyphiids are basically a sub-arctic group, adapted to moderate temperatures and high humidity (Bristowe, 1939; Gertsch, 1979; Dippenaar-Schoeman and Jocqué, 1997). In the temperate and cooler regions of the northern hemisphere, linyphiids are, in general, the dominant spiders in terms of density and species richness (Bristowe, 1941). They depend on tiny, soft-bodied insects as food source (mainly collembolans and dipterans), available on the soil surface in large numbers in the northern-temperate climate (Bristowe, 1941; Sunderland et al., 1986a; Frampton et al., 2000; Harwood et al., 2001a) and abundant in many habitats (Petersen, 1982a,b; Hopkin, 1997, 1998). Enders (1975) hypothesised that the main prey (especially collembolans) of linyphiids are less abundant in more southern regions, which would prevent the build up of larger linyphiid populations. Indeed, collembolans make up a very low percentage in the diets of spiders investigated in the subtropical and Mediterranean regions of the US, which may reflect low numbers of collembolans available as potential prey (Whitcomb, 1974; Yeargan, 1975a; Dean et al., 1987; Agnew and Smith, 1989; Hayes and Lockley, 1990; Nyffeler and Sterling, 1994). However, collembolans are a major part of the diet of some spiders in more northern areas of the US (Wheeler, 1973; Bardwell and Averill, 1997). Petersen (1982a) reviewed the literature on global geographical variation in the density of Collembola and demonstrated a latitudinal cline for grassland and forest soils, with lower densities towards the tropics. It was also shown that Collembola biomass was nearly an order of

magnitude less in tropical compared to temperate grassland (Petersen, 1982b). Collembola are poorly adapted to dry environments. Where crops in the southern US are irrigated only during the growing season, humidity at the ground surface is likely to be insufficient for Collembola during the rest of the year, making colonisation and population increase unlikely (Jürg Zettel, pers. comm.). Temperatures near the soil surface are likely to be inimical to small prey animals, especially in the southernmost states during summer, where the mean ground temperature is 32 °C, reaching at times >40 °C (Table 13). Thus, it remains possible that Linyphiidae are less abundant in the southern US than in Europe because Collembola are less abundant in the southern US.

- (3) The European studies were conducted mostly in cereal crops, which are systems with low structural diversity (they have a predominantly vertical structure). But in the US, investigations were carried out in crops with high structural diversity (i.e., cotton, soybean, peanut, alfalfa, vegetables). Structural diversity of vegetation is often associated with more diverse and species-rich spider communities (Hatley and MacMahon, 1980; Uetz, 1991; White and Hassall, 1994; Feber et al., 1998), which are not dominated by a single spider family.
- (4) Jocqué (1984) hypothesized that the scarcity of linyphiids in tropical areas is the outcome of interference competition with ants occurring in higher numbers. Dippenaar-Schoeman and Jocqué (1997) state, with regard to tropical areas,

Table 13

Aspects of the agricultural environment of spider communities in northern-temperate Europe and the southern US^a

Category	Europe	US		Information sources
Pesticide inputs in 1994 (Europe) and 1991–1994 (US) (kg ha ⁻¹)	4.2 ± 1.2 ^b	5.5 ± 1.4 ^c		World Atlas.com, FAOSTAT, NCFAP
Fertiliser inputs in 1994 (Europe) and 1998 (US) (kg ha ⁻¹)	294 ± 49 ^d	62 ± 10 ^e		World Resources Institute; Fertiliser Institute, US
Mean farm size in 1998 (ha)	17.4	206		EC, NASSUSDA
Percentage of cropland under conservation tillage in 1997/1998	<1–2	37		ECAF, Purdue News
Soil temperature in June (°C)	17.5 ± 0.47 ^f	23.9 ± 0.55 ^g	31.7 ± 0.30 ^h	HRI, UKAWC, TAMU
Soil temperature in July (°C)	19.1 ± 0.51 ^f	26.1 ± 0.22 ^g	35.7 ± 0.31 ^h	HRI, UKAWC, TAMU
Soil temperature in August (°C)	18.1 ± 0.26 ^f	26.1 ± 0.43 ^g	35.4 ± 0.54 ^h	HRI, UKAWC, TAMU
Soil temperature in September (°C)	13.9 ± 0.34 ^f	21.7 ± 0.64 ^g	26.7 ± 0.32 ^h	HRI, UKAWC, TAMU
Soil temperature in June–September (°C)	17.2 ± 0.27 ^f	24.5 ± 0.29 ^g	32.4 ± 0.36 ^h	HRI, UKAWC, TAMU
Soil temperature maximum (°C)	23.5 ^f	33.3 ^g	41.7 ^h	HRI, UKAWC, TAMU

^a EC: European Commission; ECAF: European Conservation Agriculture Federation; FAOSTAT: Food and Agriculture Organisation Statistics Database; HRI: Horticulture Research International, UK; NASSUSDA: National Agricultural Statistics Service, United States Department of Agriculture; NCFAP: National Center for Food and Agricultural Policy (Washington); Purdue News: Purdue News, February 1998; UKAWC: University of Kentucky Agricultural Weather Center, Lexington; TAMU: Texas A&M University Research and Extension Center, Stephenville.

^b Mean ± S.E. kilograms of active ingredients of insecticides, herbicides, and fungicides applied per hectare of harvested cropland for Austria, Belgium, Denmark, France, Germany, Holland, Poland, Switzerland and UK.

^c Mean ± S.E. kilograms of active ingredients of insecticides, herbicides, and fungicides applied per hectare of harvested cropland for Alabama, Arizona, Arkansas, California, Colorado, Kentucky, Louisiana, Mississippi, North Carolina, Ohio, Oklahoma, Tennessee, Texas and Virginia.

^d Mean ± S.E. kilograms of nitrogen, phosphate, and potash applied per hectare of cropland for Austria, Belgium, Denmark, France, Germany, Holland, Poland, Switzerland and UK.

^e Mean ± S.E. kilograms of nitrogen, phosphate, and potash applied per hectare of cropland for Alabama, Arizona, Arkansas, California, Colorado, Kentucky, Louisiana, Mississippi, North Carolina, Ohio, Oklahoma, Tennessee, Texas and Virginia.

^f Mean ± S.E. soil temperature, 10 cm deep, in 2001, at Wellesbourne, UK.

^g Mean ± S.E. soil temperature, 10 cm deep, in 2001, at Lexington, KY.

^h Mean ± S.E. soil temperature, 10 cm deep, in 2001, at Stephenville, TX.

“... webs built at ground level are probably so often destroyed as a result of continuous ant activity that this strategy has been almost completely abandoned. Even in temperate habitats the proportion of web-building spiders decreases markedly during periods of high ant activity”. Apart from the interference, ants have a detrimental effect on linyphiids by killing them in large numbers (Cherix and Bourne, 1980). Spider abundance on cotton in Alabama was negatively correlated with abundance of *Solenopsis invicta* (Eubanks, 2001). The interference competition hypothesis is appealing, at least for extensive areas of the subtropical region of the US where *Solenopsis* spp. occur in high numbers. Fire ants are voracious predators that build their colonies at ground level, and soil surface-dwelling spiders such as linyphiids are expected to be affected most severely. In cotton fields in east Texas, heavily infested with fire ants, these insects were observed to attack spiders aggressively by biting into a leg and clinging on to it. Ants are also known to exert a detrimental influence on spider populations in forest habitats (Cherix and Bourne, 1980; Halaj et al., 1997) and in pastures (Kajak et al., 1972). It seems, therefore, that interference competition with ants is responsible, at least in part, for the scarcity of linyphiids in field crops located within the geographic range of fire ants. The geographical range of fire ants is expanding and currently encompasses all or part of Alabama, Arizona, Arkansas, California, Florida, Georgia, Louisiana, Mississippi, New Mexico, North Carolina, Oklahoma, South Carolina, Tennessee, Texas and Virginia. The generalisation that linyphiids dominate spider communities is based on studies conducted in western, central, and Scandinavian Europe only. In Hungary (47.5°N, 19.0°E), under an eastern European continental climate, a much lower proportion of linyphiids (≈ 2 –50%) is recorded (Samu et al., 1996; Basedow et al., 2000), and this is also true for the Czech Republic (50.1°N, 14.3°E), Poland (52.2°N, 20.9°E), and Finland (60.5°N, 22.3°E) (Raatikainen and Huhta, 1968; Huhta and Raatikainen, 1974; Luczak, 1979). It is known that ants occur in considerably higher numbers in the dry climate of Hungary than in western, central, and Scandinavian Europe

(Chauvin, 1967). Interference competition with ants (sensu Jocqué, 1984) may, therefore, be the cause for the lower abundance of linyphiids in Hungarian agroecosystems.

- (5) Comparative studies in conventional and biodynamically-managed fields in Germany and Switzerland showed that the relative abundance of linyphiids rises with increasing intensity of agricultural management, whereas the relative abundance of hunters decreases (Glück and Ingrisch, 1990; Basedow, 1998; Ratschker and Roth, 1997, 1999, 2000a,b; Lukas Pffner, pers. comm.). This is also supported by the experimental work of Kajak (1978) and Kleinhenz and Büchs (1995), who demonstrated a shift to higher dominance of linyphiids associated with increased inputs of fertilisers. Similarly, Downie et al. (1998) monitored the arachnofauna in fifty agricultural grassland sites in Scotland and found that sites subject to disturbance from a high management intensity were dominated by Linyphiidae, but more stable sites had a higher proportion of non-lynyphiid families. The mechanism could be that the majority of spiders perish or emigrate from a field when it is disturbed by cultivation or an agrochemical application, but a small number of highly invasive, colonising linyphiid species (Rushton et al., 1989), return to the field rapidly, rendering Linyphiidae the dominant family. Thomas et al. (1990) showed that *E. atra* took little more than a month to substantially recolonise an insecticide-sprayed wheat field. Thus, the question arises whether the higher percentage of small linyphiids recorded in northern Europe is due to higher inputs of fertilisers and more cultivations and other agricultural manipulations compared to southern states of the US. Fertiliser inputs are four times greater in northern-temperate Europe than in southern US (Table 13) and this may contribute to the higher proportion of Linyphiidae in European studies. Nentwig (1995) also reported fertiliser usage to be low (94 kg ha^{-1}) in the US as a whole, compared with northern-temperate Europe (451 kg ha^{-1}), for 1987–1988.

US cropping systems are also characterised by greater habitat stability (with a much higher proportion of land under conservation tillage than in Europe;

Table 13) and a lower incidence of ploughing than in European systems, which typically have a rotation of cereal and break crops. Since a small proportion of linyphiid individuals may be able to survive ploughing (Duffey, 1978) and linyphiids are known to rapidly reinvade crops after disturbance (Thomas et al., 1990), they are likely to be better suited to unstable European conditions than are other groups of spider (such as the hunting spiders that form an important component of the US arachnafauna).

5.2. Population densities and biomasses

Turnbull (1973) surveyed 37 published censuses of spider abundance in a wide variety of natural and modified environments. He found an overall mean density of ≈ 130 spiders m^{-2} (range: 0.6 – 842 m^{-2}). Our estimated overall mean for European annual crops of ≈ 92 spiders m^{-2} is of the same order of magnitude as Turnbull's value. In contrast to this, the overall mean for annual row crops in the US (≈ 2 m^{-2}) is considerably lower. Spider density in perennial crops is, however, similar in Europe (52 m^{-2}) and the US (45 m^{-2}). In the search for an explanation for the large density difference in annual crops, it should first be asked whether this difference could be due to different methods being used on the two continents. In many of the US studies, spider density was assessed on the plant (Table 8), whereas in Europe density values usually refer to plant plus ground (Table 2). There even seems to be a difference, in this respect, in the way that the D-vac is used. In Europe the nozzle is pressed down vertically onto the ground, enclosing the vegetation (Samu et al., 1997), and sampling from both the ground and the plant, but in the US, crops such as cotton are often sampled by applying the nozzle to the tops and sides of plants without any contact with the ground (Dinkins et al., 1970; Gonzalez et al., 1977; Plagens, 1983; Allen Dean, pers. comm.). Riechert (1990), Halaj et al. (2000), and Greenstone (2001), who searched the ground as well as the plants, also recorded low spider densities relative to European values. This suggests that the density differences are real, and not simply an artefact of different sampling methodologies. It is noteworthy that the highest densities recorded for annual crops in southern US were found in Colorado, Kentucky and Ohio, in the northern part of the southern US (Table 11), where

ground surface conditions may not be as hot as in the deep south. A higher value, of 21 m^{-2} (not included in Table 8), was recorded by searching the ground within quadrats in 60 $m \times 70$ m experimental soybean plots surrounded by 15 m wide grass borders in Ohio (Marshall et al., 2000). The proximity of grass refuges may have resulted in higher spider densities than are typical for large commercial soybean fields.

The potential for pest control is related, in part, to spider density. Density data are comprised of adult and juvenile spiders, but juveniles are often the most abundant stage (Sunderland and Topping, 1993; Topping and Sunderland, 1998), yet are less voracious than adults. In this respect density estimates may not accurately reflect the potential for pest control. On the other hand, the majority of sampling methods underestimate the true density of spiders (Topping and Sunderland, 1994a; Sunderland and Topping, 1995; Sunderland et al., 1995).

The biomass of spiders per unit area should also be considered when comparing between continents. In the southern US, the most abundant agroecosystem spiders (*Oxyopes* spp.) had an average length of approximately 4 mm in the middle of the growing season (Nyffeler et al., 1992a) and spiders of that size have an average dry weight of 1.45 mg (Lang et al., 1997), which corresponds to 6 mg fresh weight per spider with water content of 75% (Pulz, 1987). At an overall mean density of about 2 spiders m^{-2} in crop fields of the southern US (Table 8), a spider biomass of approximately 0.012 g fresh weight m^{-2} can be expected. However, in heavily-sprayed areas, where spiders occur at extremely low densities, spider biomass is probably much lower than 0.012 g fresh weight m^{-2} . How does this compare with spider biomass in Europe? Considering an overall mean spider density in Europe of 80 m^{-2} (Table 2), and a mean fresh weight of 1.4 mg (Nyffeler and Benz, 1988a), the average spider biomass is approximately 0.112 g fresh weight m^{-2} in European crop fields. Thus, both density and biomass of spiders per square meter in annual crops appear to be higher in Europe than in the US. Biomass can be nearly an order of magnitude higher in crop fields in Europe compared to southern US, suggesting that energy flow through spider communities of agroecosystems may also be greater in Europe.

The greater spider density and biomass in Europe may be attributable to the high reproductive capacity

exhibited by a small number of species in the genera *Erigone*, *Oedothorax*, and *Lepthyphantes*, which is part of a suite of adaptations enabling the rapid exploitation of pioneer habitats, including agriculture (Nyffeler, 1982; Sunderland, 1991, 1996; Sunderland and Topping, 1993; Sunderland et al., 1996; Topping and Sunderland, 1998; Blick et al., 2000). It has been suggested that, possibly, by accident of geography, there may be no ecologically equivalent linyphiids in the US with the capability to build up high numbers in agroecosystems (Greenstone, 2001). *L. tenuis* does occur in some parts of the US, but is a recent introduction from Europe (Edwards, 1986), and it is too soon to know if it will significantly increase spider densities in US fields. *L. tenuis* is also present in New Zealand (probably introduced accidentally from Europe) and now dominates the agricultural arachnafauna, but at a density five times less than in Europe (Topping and Lövei, 1997). This fits the hypothesis that linyphiids prosper less well at southern latitudes, since Wellington (New Zealand) at 41.3°S latitude has a mean annual temperature of 12.7°C. Overall spider density, however, does not appear to be related to latitude in a simple way, since Aguilar (1977) recorded densities in cotton in Peru (relatively close to the equator at 12°S latitude) of 15–45 m⁻², i.e. intermediate between southern US and northern Europe.

Since hunting spiders that are cannibalistic and eat other spider species are very common in US fields (Hurd and Eisenberg, 1990; Nyffeler, 1999), the question arises as to whether their araneophagy prevents them from building up high population densities. Spiders eating spiders can, indeed, have a limiting influence on spider density as Schaefer (1974) has demonstrated in an experimental study, but the mortality rates due to araneophagy do not appear to be high enough to explain the huge difference in numbers between Europe and the US. Where fire ants are particularly abundant, they seem to negatively affect the density of spiders through intraguild predation and interference competition (Wilson and Oliver, 1969; Ali et al., 1984; Eubanks, 2001), but no rigorous evidence has been published to date.

Spider abundance could be related to pesticide inputs, with direct effects on survival and natality of spiders and indirect effects operating through the food supply (Jepson, 1989; Sunderland, 1992). However, pesticide inputs in Europe and the US were rather

similar (Table 13), suggesting that pesticides may not be the main cause of differences in spider density.

It can be argued that the structure of agricultural landscapes will influence spider abundance (Landis et al., 2000; Sunderland and Samu, 2000). If an area is divided into relatively small units that differ in habitat type, and in the timing and nature of management activities, then spider populations may have more opportunities to find suitable overwintering sites (Desender et al., 1989) and temporary refuges (Halaj et al., 2000; Lee et al., 2001). Modelling studies suggest that diversified agricultural landscapes support a greater mean density of spiders than do more homogeneous landscapes (Topping and Sunderland, 1994b,c; Halley et al., 1996; Thomas, 1996; Topping, 1997, 1999), and spider density can be negatively correlated with field size (Raatikainen and Huhta, 1968). Similarly, the rate of spider recolonisation of land after treatment with pesticides is negatively correlated with the area of land treated (Duffield and Aebischer, 1994). If mean farm size can be used as an indicator of landscape diversity, agricultural landscapes are probably more diverse in Europe than in the US. Mean farm size in the US in the last decade has been consistently above 100 ha (cf. EU highest national mean of 70 ha), and mean farm size in 1998 was an order of magnitude greater in the US than in Europe (Table 13). This could account for the low spider density in the US.

The ground below open annual row crops in the southern US can become extremely hot and dry during summer (Table 13), and this is likely to be inimical to ground-dwelling spiders and their prey, especially Collembola (Draney and Crossley, 1999; Jürg Zettel, pers. comm.). When more ground cover is available, in the form of denser crops such as alfalfa and pasture (Table 8), or by intercropping (Sunderland and Samu, 2000), or as experimental mulches or straw refuges (Riechert and Bishop, 1990; Halaj et al., 2000), spider density increases to European levels. In natural habitats, where ground-dwelling spiders are also protected from the worst exigencies of climate, densities of spiders in the southern US can peak at up to 1000 m⁻² (Pearse, 1946; Moulder and Riechle, 1972). In European forest habitats densities of 50–500 m⁻² are typical (Kirchner, 1964; Ellenberg et al., 1986; Schaefer and Schauer mann, 1990), and similar values are reported for forests in the US (Pearse, 1946; Gasdorf and Goodnight, 1963; Moulder and Riechle,

1972). We therefore suggest that a major cause of low spider density in southern US is the lack of protection from heat and drying on the ground. If this interpretation is correct, the prognosis for improving biological pest control by spiders in tropical and sub-tropical regions is good, providing that practical and economic solutions to increasing ground cover can be found.

5.3. Prey selection

Agroecosystem spiders feed infrequently (Nyffeler et al., 1994a), and only $\approx 3\text{--}8\%$, in both European and US fields, are observed to be feeding at any given time (Table 5). Predation rates (per day) depend on factors such as spider size, age, sex, physiological events in the spider's life, weather conditions, and on prey availability (Nyffeler et al., 1994a). Based on the percentage of spiders holding prey, average handling time, and diel activity period of the spider, it was estimated that a typical agroecosystem spider in the US captured ≈ 1 prey organism per day (Nyffeler et al., 1994a). European agroecosystem spiders have also been estimated to capture ≈ 1 prey per day (Nyffeler and Benz, 1988a,b; Nyffeler and Breene, 1990). In the laboratory, the same species feed at a rate several times higher when food is offered ad libitum (Lingren et al., 1968; Muniappan and Chada, 1970b; Young and Lockley, 1986; Bumroongsook et al., 1992). This suggests that field spiders consume prey at rates below their maximum feeding capacity. Field spiders were often observed in an underfed condition in the US and Europe, and this applied especially to spiders that forage without a web (Nyffeler and Breene, 1990; Wise, 1993). Even web-making linyphiids in cereals appear to be hungry most of the time. Bilde and Toft (1998), for example, showed that *E. atra* was at a hunger level equivalent to 7 days starvation throughout June. Similarly, Harwood (2001) determined the field condition of female *L. tenuis* to be consistent with a feeding rate equivalent to less than one *Drosophila melanogaster* per day, which is sub-optimal for reproduction. Compared to other poikilotherms of equal body weight, spiders generally have very low metabolic rates, and also possess the capacity to reduce them further during periods of starvation (Greenstone and Bennett, 1980). Turnbull (1973) stated that feeding by spiders is erratic, with short intervals of intensive feeding

interspersed with periods of fasting. An extensive digestive system, distensible abdomen, and capacity to store fat, allows them to feed to excess when food is abundant, yet survive without food for long periods when prey densities drop to low levels (Riechert and Harp, 1987; Foelix, 1996). However, spiders can increase their predation rates and show a functional response during severe outbreaks of insect pests (Provencher and Coderre, 1987; Breene et al., 1990). Predation rates obtained in the field under conditions where prey are rare may therefore greatly underestimate predation rates where prey are abundant (Nyffeler et al., 1994a).

Laboratory feeding experiments, using a variety of spider species and crickets as model prey, revealed that the optimal prey length was 50–80% of the length of the spider (Nentwig, 1987), a conclusion supported by field observations (Nyffeler et al., 1994a). Spider individuals of small biomass dominate the faunas in field crops of both Europe and the US, and feed primarily on tiny prey organisms (<4 mm long) (Young and Edwards, 1990; Alderweireldt, 1994; Nyffeler et al., 1994a).

The prey spectrum of spiders in European crop fields is very uniform, comprising almost exclusively tiny, soft-bodied insects from the orders Collembola, Diptera, and Homoptera (Sunderland et al., 1986a; Nyffeler and Benz, 1988a,b; Alderweireldt, 1994; Jmhasly and Nentwig, 1995). So far there is a single quantitative study from the US, in which a prey spectrum resembling somewhat the one from Europe has been described. Bardwell and Averill (1997) reported a prey spectrum consisting primarily of Collembola, Diptera, and Homoptera (leafhoppers) for spiders in cranberry bogs in Massachusetts (Table 14). With a mean annual temperature of $\approx 9^\circ\text{C}$, the study area in Massachusetts is subject to a humid continental climate comparable to the northern-temperate climate of Europe (Table 11).

Most US field studies were conducted in subtropical or Mediterranean climates (Table 9), with a distinctly higher mean annual temperature ($\approx 13\text{--}20^\circ\text{C}$) than the northern-temperate zone of Europe (Table 11). As in Europe, spiders in US field crops feed predominantly on tiny prey. However, the prey composition in US crops is considerably more diverse than in Europe (cf. Tables 3, 4 and 9). The following factors could play a role:

Table 14

Percentages of five prey types in the diets of spiders in cranberry bogs in Massachusetts, US (modified after Bardwell and Averill, 1997)

Prey type	Lycosidae (<i>Pardosa</i> spp.)	Oxyopidae (<i>O. salticus</i>)	Tetragnathidae (<i>T. laboriosa</i>)	Other species	All spiders
Diptera	42.4	23.5	62.5	35.9	39.4
Collembola	21.2	35.3	12.5	9.4	18.6
Homoptera	9.1	11.8	16.7	12.5	11.7
Araneae	12.1	0.0	0.0	7.8	6.9
Other	15.2	29.4	8.3	34.4	23.4

- (1) There is a general trend for species richness to increase towards the equator (Hillebrand and Azovsky, 2001) suggesting that a greater breadth of spider diet (reflecting a more diverse composition of potential prey) can be expected in the southern US compared to northern Europe.
- (2) The European studies were conducted mostly in cereal crops, whereas in the US crops with higher structural diversity were targeted. Based on theory (MacArthur and MacArthur, 1961; Pianka, 1966; Greenstone, 1984) higher diet breadth is predicted in systems with higher vegetation structural diversity. Also, more variation in the feeding patterns of spiders can be expected in the US, since a greater variety of different types of crops were studied there.
- (3) In European fields, a single spider guild (linyphiids with low diet breadth) dominates. Spider guild structure in US field crops is much more complex and encompasses a higher percentage of hunting spiders with high diet breadth, resulting in a higher overall mean diet breadth (Nyffeler, 1999).

5.4. Spiders as predators of pests

European reports on the predatory role of spiders refer largely to their potential as enemies of aphids (Nyffeler and Benz, 1982; Sunderland, 1987, 1988). Some 20–30 aphids m^{-2} per day are killed at times by soil surface-dwelling spiders in the field. If mortality rates of this order were to occur early in the growing season, small linyphiids could have an inhibitory effect on aphids by slowing down their early rate of increase, thus acting as ‘stabilising agents’ (Riechert and Lockley, 1984). The observation by several researchers that these spiders rarely feed on predaceous arthropods (usually <10% of their diet) (Table 10) enhances their appropriateness as biological control

agents. After reviewing the agroecology of *L. tenuis*, Sunderland (1996) listed 12 attributes (including diet, ubiquity, abundance, voracity, and mobility) suiting it to biocontrol.

The role of spiders as aphidophages has also been considered in the US (Muniappan and Chada, 1970a; Horner, 1972; Bumroongsook et al., 1992). The majority of US studies, however, have investigated the role of spiders as predators of lepidopteran and heteropteran pests. This may be explained by the fact that hunters, the numerically dominant spider predators in most US fields, have excellent capabilities to track down and seize lepidopteran and heteropteran prey. The biocontrol potential of these spiders is, however, limited by their involvement in intraguild predation, by infrequent feeding (Table 5), and by their low density in the field (Table 8). It is assumed that spider populations, at densities of $\approx 2 m^{-2}$, are incapable of exerting any significant biological control on insect pests in US crops (Greenstone, 2001). Therefore attempts have been made to artificially increase spider density in US field crops by habitat manipulations, such as creating straw shelters as temporary refugia (Riechert and Bishop, 1990; Tuntibunpakul and Wise, 1998; Halaj et al., 2000). In such experiments spider density was increased to $\approx 300 m^{-2}$ (comparable to the density in some European fields, Table 2), resulting in enhanced predation and a significant reduction of plant damage (Riechert and Bishop, 1990; Halaj et al., 2000).

6. Conclusions

Similarities and differences between the insectivorous activities of agroecosystem spiders on the two continents (Table 15) may be summarised as follows.

Small web-building spiders (Linyphiidae), that live near the ground, numerically dominate in field crops of northern-temperate Europe. They have a narrow diet,

Table 15
 Characteristics of the arachnofauna of agroecosystems: comparisons between northern-temperate Europe and the US

Characteristic	Europe	US
Dominant spider taxa	Linyphiidae	Several families (varying between studies)
Spider density	High	Low
Spider size	Small	Small
Main microhabitats occupied	Soil surface	Vegetation and soil surface
Main foraging strategy	Sheet web	Hunters
Feeding frequency	Low	Low
Prey size	Small	Small
Diet breadth	Narrow	Wide
Predation of lepidopteran/heteropteran pests	Low	High
Predation of aphids	High	Probably low
Predation of spiders and predaceous insects (i.e. intraguild predation)	Low	High

feeding mainly on tiny, soft-bodied insects, including a high percentage of pest aphids. Their biocontrol potential may be somewhat limited due to low feeding frequency. Nevertheless, because they can build up huge populations (up to 600 m^{-2}), and because of a low incidence of intraguild predation, these spiders are assumed to play an important ecological role as stabilising agents, slowing down the population explosion of some insect pests such as harmful aphids.

In contrast, hunting spiders from several families (e.g., Oxyopidae, Salticidae, Thomisidae and Lycosidae), mostly of small body size, numerically dominate the spider faunas in many US field crops. Like their European counterparts they feed primarily on tiny insects, but their diets also include larger insects and spiders. Potentially, they are highly beneficial because of their efficient foraging behaviour enabling them to discover and seize smaller instars of various species of lepidopteran and heteropteran pests. Their value as biocontrol agents is, however, limited, due to low density, infrequent feeding, and involvement in intraguild predation.

Impact on pest populations is dependent, in part, on spider density and biomass, which is considerably greater in Europe than the US. Mean farm size is an order of magnitude less in Europe than in the US and this is likely to be associated with greater habitat diversity, which is known to increase spider abundance.

However, many of the contrasts between continents in insectivorous activities of agroecosystem spiders are attributable to climatic differences, most of the US data originating from more southern latitudes (i.e., subtropical and Mediterranean climates) with higher mean annual temperatures compared to northern Europe. There is a dearth of field studies from southern Europe under Mediterranean climates and the northern regions of the US under humid continental climates. Little is known about the insectivorous activities of agroecosystem spiders in New England, the northwestern, and the midwestern states of the US. The sparse data that are available from southern Europe and the northern US hint that patterns of spider predation may differ less between the two continents than reported here, if study areas of similar latitude and mean annual temperature could be compared. In terms of biological control of crop pests, the comparison between continents is more directly valid since a large proportion of the productive agricultural land area of Europe is located in more northern latitudes (approximately 405.7 million ha of arable land plus permanent pasture in northern Europe and 117.4 million ha in the south—World Atlas.com) compared to the US, where there are about 128.4 million ha in states above 40°N , but 199.1 million ha in the south (USDA Economic Research Service). Nevertheless, there is clearly substantial agricultural production in southern Europe and northern US and researchers are urged to investigate the role of spiders in these regions too.

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