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Six-year Malaise trapping of the leaf miner *Chromatomyia fuscula* (Diptera: Agromyzidae) and its chalcidoid parasitoid complex in a barley field and its boundary

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Malaise, parasitoid, Chalcidoidea, *Chromatomyia fuscula*, Agromyzidae, barley, boundary, leaf miner

Abstract. The univoltine leaf miner *Chromatomyia fuscula* (Zetterstedt) (Diptera: Agromyzidae) is a regular cereal pest in Scandinavia. The fly and its most important parasitoids were studied in a 15.5 ha organically-grown field in southern Norway. Each year (1992–1997), one Malaise trap was placed in the spring barley part (2.5 ha) of the field, and (except for 1994) another along the nearest wooded boundary for the whole season. Because of crop rotation, the traps changed position every year. *C. fuscula* and 15 parasitoid species previously reared from *C. fuscula* were sorted from the catches.

Few *C. fuscula* were trapped in the boundary, suggesting that at least the lower vegetation strata were unimportant for the overwintering fly (*C. fuscula* overwinters as an adult). The parasitoid complex was remarkably stable over years, and 13–15 of the species were found each year (habitats combined); 0–6 of the species were not found in both habitats each year. Only 4 species attained fractions higher than 10% of the total annual catches in both habitats during the 6 years: the larval parasitoids *Diglyphus begini* (Ashmead) and *Hemiptarsenus unguicellus* (Zetterstedt), and the pupal parasitoids *Cyrtogaster vulgaris* Walker and *Chrysocharis pubicornis* (Zetterstedt). In the boundary, *C. vulgaris* dominated every year (43–83%). In the crop, this species alternated with *D. begini* (1992, 1994) or *H. unguicellus* (1997) as the dominant species.

In most years, the catches of both the leaf miner and its parasitoids were larger in the crop than in the boundary, but the species number and composition were fairly similar in the two habitats. The parasitoid diversity (Shannon-Wiener H') tended to be higher in the crop (0.8–2.0) than in the boundary (0.8–1.8). Correspondingly, the evenness (both Shannon-Wiener J' and species rank on ln abundance) was higher, and the dominance (Berger-Parker) lower, in the crop than in the boundary. Every year, overwintered *C. fuscula* invaded the crop, but only in 1993 and 1997 did the trapping reveal a distinct next generation, suggesting a very high pre-adult mortality the other years. In 1993 and 1997, *C. vulgaris* and *D. begini* had rather similar abundances in the crop, and the lowest combined fractions (less than 60%) of the years, leading to the highest diversity and the lowest dominance through the 6 years (in both habitats).

Our results indicate that the boundary was part of the parasitoids' foraging/overwintering area, and that the boundary was more important to the parasitoids than to their leaf miner host. Boundaries therefore seem to be important for the control of *C. fuscula*.

INTRODUCTION

The leaf miner *Chromatomyia fuscula* (Zetterstedt) is a regular agricultural pest in Scandinavia. It attacks cereals and grasses, and densities of c. 50,000 larvae/m^2 have been reported in spring barley. The fly is univoltine and overwinters as an adult in unknown habitats (Andersen, 1991). Little was known about the species composition and influence of the parasitoids of *C. fuscula* until 1991, when a 7-year project was started to study the fly and its parasitoid complex in a barley crop in southern Norway. The barley crop was part of an organically-grown field, and possible effects of pesticides could therefore be eliminated. The study was also motivated by the fact that the fauna and biology (host species, geographic distribution, phenology, etc.) of parasitic Hymenoptera in general are poorly known in Norway (Ottesen, 1993).

The project included sampling of infested plants (1991–1995; some preliminary results given in Hågvar et al., 1994), experiments with trap plants (1993 and 1995; Trandem, 1998a), and continuous Malaise trapping (1992–1997) in the barley crop and its boundary. Malaise data on phenology and sex ratio of each parasitoid species will be presented elsewhere (Hågvar et al., unpubl.). In the present paper, we will focus on the total Malaise catches in the barley crop, to identify the composition of the parasitoid complex and to study the stability of this complex (both in absolute and relative terms) over a period of six years. Field boundaries are important habitats for parasitoids on agricultural pests, by providing shelter, alternative hosts, food for adults, hibernation sites etc. (see Altieri et al., 1993, for an overview). We wanted to know to what extent *C. fuscula* and its parasitoids used the boundaries, by comparing the catches in the two habitats with respect to (1) the fly and parasitoid abundance; and (2) the size and composition of the parasitoid complex.

MATERIAL AND METHODS

In South Norway, overwintered *C. fuscula* invade the fields to oviposit in May–June. The larvae pupate in the leaf and emerge as adults 5–7 weeks after oviposition; the development from egg to adult requiring about 400 degree-days (Andersen & Fugleberg, 1997). Our study site was the 15.5 ha organically-managed field "Frydenhaug" at Ås, 30 km south of Oslo (Fig. 1). The field had a 6 course crop rotation, each crop covering a rectangle of about 2.5 ha (barley crop 1.3 ha in 1996). The eastern and southern margins of the field were forested. A semi-natural boundary strip with grasses lay between the field and the forest. *C. fuscula* was the dominant cereal leaf miner (99%) in the studied area (Andersen, 1991), and its mines could be found in grasses in the boundary and grass crops, as well as in the spring barley in the barley crop. No other leaf miner was as numerous as *C. fuscula* in the area, except for the aspen leaf miner *Phyllocnistis labyrinthella* (Bjerkander) (Lepidoptera: Gracillariidae) (E. Hågvar and N. Trandem, pers. obs.). *P. labyrinthella* and *C. fuscula* have two parasitoids in common: *Cirrospilus vittatus* Walker and *Chrysocharis pentheus* (Walker) (Sundby, 1957; Hågvar et al. 1994; Trandem 1998c).

All 6 years (except 1994), two Malaise traps sampled throughout the season. One was placed along the forested boundary of that year's barley crop, and one in the barley crop itself, 60 m from the boundary (Fig. 1). Because of the crop rotation, the barley crop and the boundaries changed position within the field each year (Fig. 1). If the grassy boundary strip was broad enough (about 4 m, eastern side of the field), the boundary trap was placed there (1995). This is referred to as "grass boundary" later, and was dominated by *Festuca pratensis*, *Phleum pratense*, *Poa glomerata*, *Lolium multiflorum*, and *Agropyron repens*. In addition thistle (*Cirsium arvense*) and stinging nettles (*Urtica*) were abundant in patches. If the grassy boundary strip was very narrow (southern side of the field, with an open ditch separating forest and boundary strip), the boundary trap was placed among the deciduous trees (*Populus tremula*, etc.) just on the other side of the ditch. This is called "forest boundary" later. The snow melted considerably slower in the forest boundary (facing north) than in the grass boundary (facing west). In 1994, there was only one trap, and this was placed in the barley crop. In 1997, the boundary trap was placed in the grass boundary, adjacent to the 1997 green fodder crop instead of the barley (Fig. 1) because the nearest boundary in 1997 lacked continuous forest.

The traps were black and did not discriminate between flying directions of the insects. The longitudinal axis was parallel with the boundary, to collect insects moving into or out of the crop, and the capture zone was about 1 m high. The crop trap was parallel to the boundary trap. Collecting bottles contained 70% alcohol and were emptied at least once a week, depending on year and time of the season. Continuous weather data (temperature, precipitation etc.) were available from a station 1 km away (Table 1). In

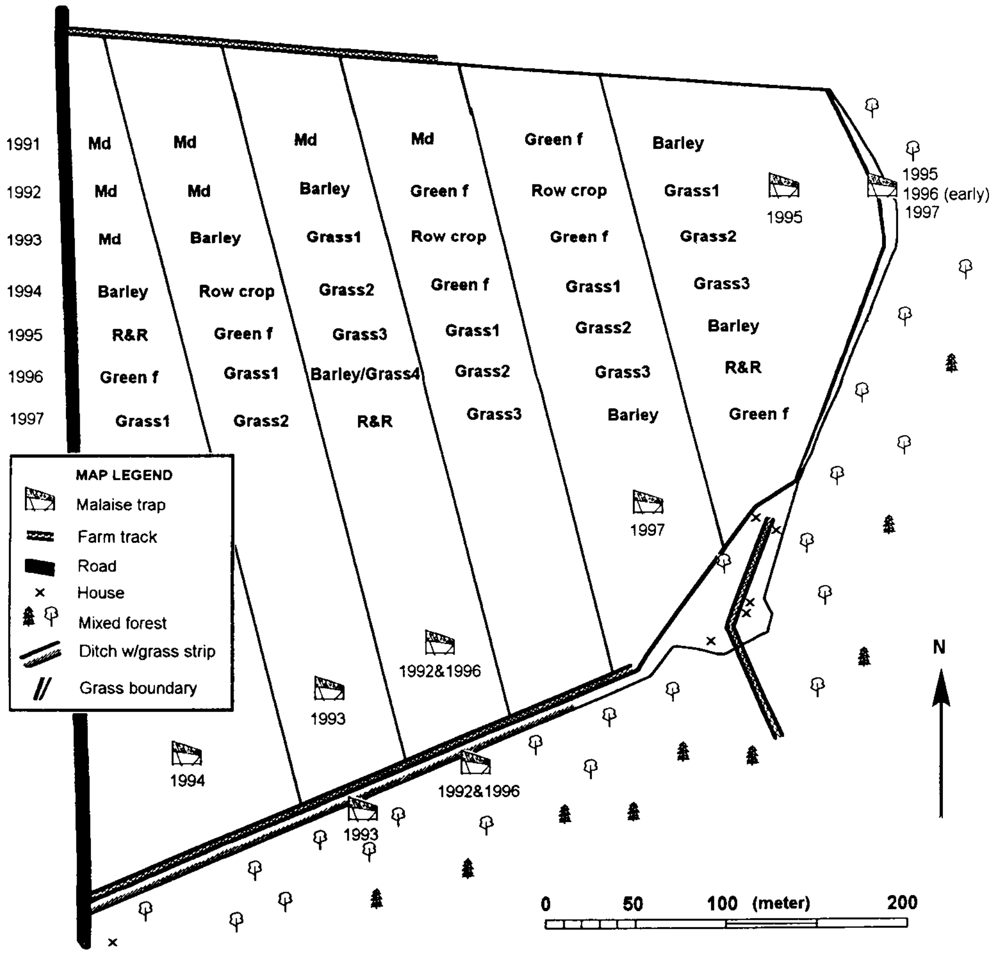

Fig. 1. The "Frydenhaug" field and its two types of boundary, with annual location of the six crops and the Malaise traps shown. Md – original meadow preceding organical growing, which started in 1991; Barley – spring barley crop undersown with grass/clover mixtures; Green f – green fodder (barley and peas 1991–95; oats and peas 1996–97; from 1993 undersown with grass/clover mixture); Row crop (only in 1992–94) – 1992–93: beet/rape/oats/barley; 94: as in 93 but not beet); R&R (1995–97) – rape/ryegrass; Grass 1–4 – grass 1st to 4th year (timothy, meadow fescue, smooth meadow grass, white clover, red clover, ryegrass).

general, the sampling period covered the period from around sowing or germination early in May to thrashing in August/September (crop trap) or several weeks later (boundary trap, crop trap in some years). In 1996, an additional trap was placed in the grass boundary (bordering last year's barley crop) for some weeks early in the season (April and May), starting about 1 month before the barley was sown and with the soil still frozen.

More than 20 chalcid and at least two braconid parasitoids are known to parasitize *C. fuscula* in Norway (Hågvar et al., 1994; Trandem, 1998b). Of these, 15 chalcid species/species-groups were included in this study; i.e., they were sorted out from the Malaise material and counted. The species excluded were rare on *C. fuscula* in the study area (Hågvar et al., 1994), and some of them were also difficult to identify correctly: all braconids, the pteromalids *Stictomischus* sp., *Miscogaster* sp.(p?), *Trichomalopsis* sp. and *Callitula bicolor* Spinola, plus the eulophid *Closterocerus lanassa* (Walker). Excluded was also the eupelmid *Eupelmus vesicularis* (Retzius), which was discovered as a *C. fuscula* parasitoid only in 1995 (going through the material again would have taken disproportionate amounts of time). Two species were identified to species-group, but for simplicity they are referred to as species later: *Pediobius metallicus* (Nees) [formerly *P. acantha* (Walker); Graham, 1993], which was not distinguished from other species in the *P. epigonus* group (Bouček, 1965), and *Diglyphus minoeus* (Walker), which were mixed with *D. chabrias* (Walker). Note that *D. begini*, the most common *Diglyphus* species in the catches, has been considered a Nearctic/Neotropical species (e.g. Heinz & Parella, 1990). However, the species has been recorded from Europe several times (Compton, 1981; Hågvar et al., 1994; C. Hansson and J. LaSalle, pers. comm.), and its identity in the present study has been confirmed by J. LaSalle.

TABLE 1. Average monthly temperature (°C) and precipitation (mm) near the study site at Aas in 1992–1997. Below: Norm = average values for 1961–1990 (Meteorologiske data for Ås, Agricultural University of Norway, Department of Agricultural Engineering).

Year	April		May		June		July		August		September		October	
	temp	precip	temp	precip	temp	precip	temp	precip	temp	precip	temp	precip	temp	precip
1992	3.8	66.4	12.8	49.1	17.3	16.7	16.2	88.4	13.9	153.5	10.9	55.4	2.7	31.4
1993	5.8	32.2	12.6	51.9	13.4	34.6	14.6	86.2	12.9	109.1	8.5	30.9	4.1	151.4
1994	6.3	81.5	10.7	4.9	13.5	49.2	19.7	4.3	15.8	158.3	9.8	115.7	5.1	48.7
1995	3.7	52.0	9.4	47.2	14.5	133.7	16.0	157.9	17.0	23.5	11.0	97.9	9.0	55.6
1996	4.3	15.1	8.3	65.5	13.7	48.5	15.0	29.6	17.1	73.9	9.3	85.5	7.7	147.5
1997	4.5	6.5	9.1	56.5	15.8	61.2	18.4	69.0	19.9	63.4	12.1	82.4	4.2	87.5
Norm	4.1	39.0	10.3	60.0	14.8	68.0	16.1	81.0	14.9	83.0	10.6	90.0	6.2	100.0

A total of 51,600 specimens were sorted out, including the host, *C. fuscula*, which made up 22% of the catches. The following indices were calculated for the pooled catch of relevant parasitoids in each habitat and year (see Tokeshi, 1993):

– Species richness S: the total number of parasitoid species.

– Shannon-Wiener diversity index H' (= $-\Sigma(p_i \cdot \ln p_i)$, where p_i is the relative frequency of species i). This index has several drawbacks (Southwood, 1995), but can still be useful if the results are interpreted with caution (Lockwood et al., 1996).

– Shannon-Wiener index for evenness J' (= H'/lnS).

– Berger-Parker dominance index d (= N_{max} /N, where N_{max} is the number of individuals belonging to the most abundant species, N = total number of specimens).

– Evenness expressed as a graph with species rank against ln abundance, useful for a small number of closely related species.

RESULTS

The sampling periods and annual catches of *C. fuscula* and each parasitoid species are given in Table 2. If nothing else is stated, all results are for the full sampling period in each habitat.

Annual abundances and differences between crop and boundaries

The terms "annual abundance" and "annual catch" are used interchangeably to mean the total catch of either flies or parasitoids in one trap in one year. Phenology of the Malaise catches (two examples shown in Fig. 2) implied that the catches of *C. fuscula* mostly

TABLE 2. Relative frequencies (%) of chalcid parasitoids of *Chromatomyia fuscula* sampled by Malaise traps in a barley crop and its forest boundary (Fo-Bo) or grass boundary (Gr-Bo) during 6 years. An entry of 0 means a relative frequency in the interval <0, 0.5>; a dash means the species was not found in the catches. The parentheses in the totals give the difference in abundance (or species number) between the total sampling period and the sampling period the two habitats had in common that year.

Year	1992	1992	1993	1993	1994	1995	1995	1996	1996	1996	1997	1997
Habitat	Fo-Bo	Crop	Fo-Bo	Crop	Crop	Gr-Bo	Crop	Gr-Bo	Fo-Bo	Crop	Gr-Bo	Crop
Sampling period	7.5.–29.10.	13.5.–2.9.	5.5.–3.11.	10.5.–20.8.	16.5.–8.8.	2.5.–12.9.	16.5.–25.8.	23.4.–11.6.	23.4.–15.10.	11.6.–15.10.	8.4.–11.11.	8.4.–11.11.
Barley sown/thrashed		8.5./2.9.		30.4./20.8.	6.5./10.8.		6.5./28.8.			15.5./6.9.		23.4./11.8.
Larval parasitoids:												
Diglyphus begini (Ashmead)	6.5	81.2	12.2	22.1	71.5	4.6	13.8	–	7.4	24.3	6.0	11.7
D. isaea (Walker)	–	0.1	0.1	–	–	0.3	0.9	–	1.8	1.7	0.3	0.1
D. minoeus/chabrias (Walker)	0.2	0.6	1.1	9.3	1.3	–	1.2	–	0.2	0.9	0.1	2.7
Hemiptarsenus unguicellus (Zetterstedt)	2.0	3.2	5.6	16.9	1.8	3.2	7.5	–	5.6	3.7	15.7	25.3
Pnigalio soemius (Walker)	3.3	0.7	1.4	1.1	0.3	1.0	1.7	–	4.1	0.9	3.4	1.6
Neochrysocharis aratus (Walker)	0.4	0.8	1.5	0.9	4.0	0.5	1.6	–	1.8	1.6	0.7	19.5
N. formosa (Westwood)	0.2	–	–	–	0.1	–	–	–	–	–	0.2	0.5
Cirrospilus vittatus Walker	2.0	–	2.7	0.8	0	0	–	–	0.2	0.1	0.8	1.4
Chrysocharis pentheus (Walker)	–	0.1	0.6	0	0.1	–	–	–	0.2	–	0.3	0
Larval-pupal parasitoids:												
Chrysocharis polyzo (Walker)	0.2	0.1	0.2	0.5	0.1	0.1	0.1	–	–	0	1.1	0.3
C. orbicularis (Nees)	–	0.2	1.6	6.1	0.1	0.1	0.2	–	0.6	0.5	3.5	2.9
Halticoptera circulus (Walker)	–	0.2	9.5	0.3	0.3	0.3	5.3	–	0.2	0.1	0.4	3.9
Pupal parasitoids:												
Chrysocharis pubicornis (Zetterstedt)	0.2	1.4	1.4	4.0	5.1	1.6	8.6	–	3.7	10.5	14.1	15.2
Pediobius spp.	3.9	1.6	1.7	2.5	0.7	5.2	4.2	–	0.4	1.1	10.1	1.2
Cyrtogaster vulgaris Walker	81.1	9.8	60.4	35.5	14.6	83.1	54.9	100	73.9	54.6	43.4	13.8
Total parasitoid individuals	508 (–51)	1,768	1,158 (–885)	2,074 (–53)	23,435	2,367 (–899)	891	572	514 (–78)	2,398	1,985	2,645
Total parasitoid species	11 (–1)	13	14 (–1)	13	14	12 (–1)	12	1	13	13	15	15
Total *Chromatomyia fuscula* individuals	130 (–13)	445	226 (–8)	1,801	2,623	244 (–11)	666	65	26 (–10)	1,553	100	3,405

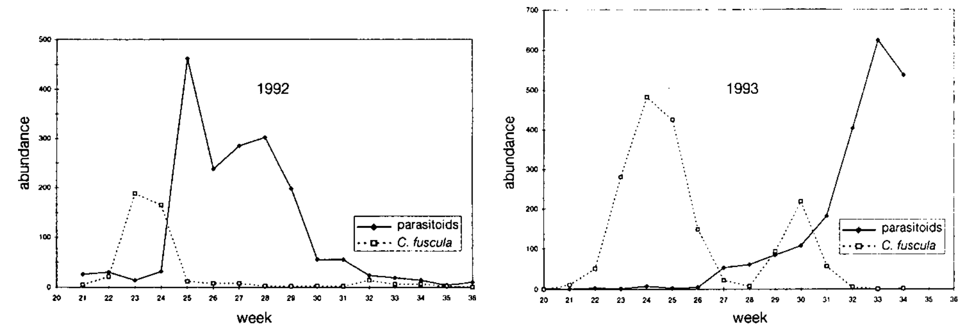

Fig. 2. Weekly Malaise catches of adult *C. fuscula* and its parasitoids in the barley crop during two of the years (see Table 2 for exact dates of trapping period).

represented immigrating, overwintered flies (F_0), except in 1993 and 1997, when a small (20% in 1993) or large (78% in 1997) fraction seemed to belong to the emerged F_1 generation. Conversely, the parasitoid catches seemed to represent the F_1 generation, except for some overwintering *Cyrtogaster vulgaris* (see discussion). In the crop, there was a positive correlation between the annual abundance of F_0 flies and F_1 parasitoids (Fig. 3).

In all years except 1997, the traps collected more parasitoids than flies (Table 2). The annual fluctuations appeared to be largest in the parasitoid catches from the crop (891-23435); in 1994 the number of parasitoid specimens sampled was 9 times higher than in any other year, and 26 times higher than the year after. The fluctuations of the fly catches in the crop were considerably smaller (445-3405), with the lowest value in 1995, the year after the high parasitoid abundance. In the boundary the catches of parasitoids showed moderate fluctuations (508-2367), and few flies were captured (26-244).

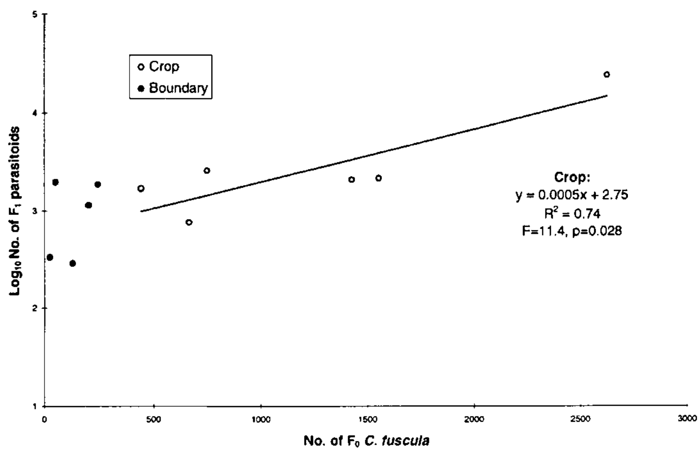

Fig. 3. Malaise catches of F_0 *C. fuscula* (i.e. flies immigrating in the spring) versus F_1 parasitoids the same year (assumed to have developed on the progeny of these flies). Catches from 6 (crop) or 5 (boundary) years. The regression of boundary data was not significant (r^2 = 0.17, F = 0.6, p = 0.5). Specimens were allocated to the F_0 and F_1 generation on the basis of the phenology (cf. Fig. 2); start of F_1 emergence was verified by inspections of *C. fuscula* mines from the field.

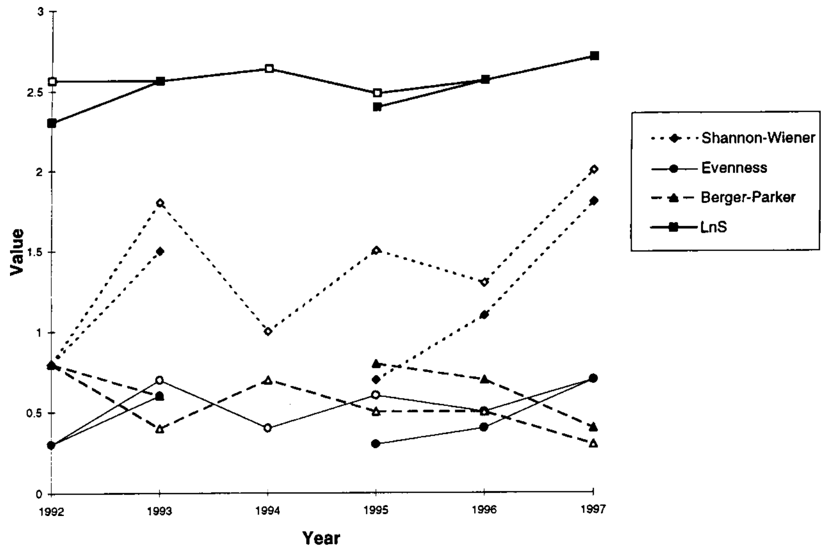

Fig. 4. *C. fuscula* parasitoid species number (Ln transformed to fit scale) and other diversity indices calculated from the total annual catches in crop (open symbols) and boundary (filled symbols), respectively. Malaise trap data from 6 years; boundary was not sampled in 1994. All years except 1994 have eight symbols, of which some are overlapping.

Fly and parasitoid abundance were always higher in the crop trap than in the boundary trap, except for parasitoids in 1995. For the flies, the boundary catches made up 2–37% (pooled mean 9%) of the crop catches. The maximum boundary fraction of 37% was found in the grass boundary in 1995, but in the same boundary two years later (Fig. 1), the fraction was much lower (3%). For the parasitoids, the boundary catches made up 21–75% (excluding 1995, pooled mean 47%) of the crop ones. Also the parasitoids had the highest boundary fraction in 1995, when the boundary abundance of parasitoids was almost 3 times higher than the crop one (or 1.6 times higher in the common sampling period). Two years after, the same boundary had lower parasitoid abundance than the crop (but still 75%). If the traps caught representative samples of both flies and parasitoids, it is concluded that *C. fuscula* uses the crop boundaries less frequently than its parasitoids.

The abundance in crop and boundary was positively correlated for most parasitoid species (Spearman $r > 0.3$ in 13 out of 15 species; $n = 5$ years in each test; $p = 0.008$, two-tailed binominal test, $n = 15$ correlations). Two species had a negative r_S, and interestingly, these were the two most numerous ones: *C. vulgaris* and *Diglyphus begini*. The host *C. fuscula* also had a negative coefficient. None of the 16 correlations were statistically significant in their own right.

Structure of the parasitoid complex in different years and habitats

In total, all the 15 species included in the study were trapped in both habitats, and the species list varied little from year to year (Table 2). Crop and boundary had at least 9 species in common each year. *Cirrospilus vittatus* was the only species that more than one year was sampled from only one and the same habitat (boundary 1992, 1995).

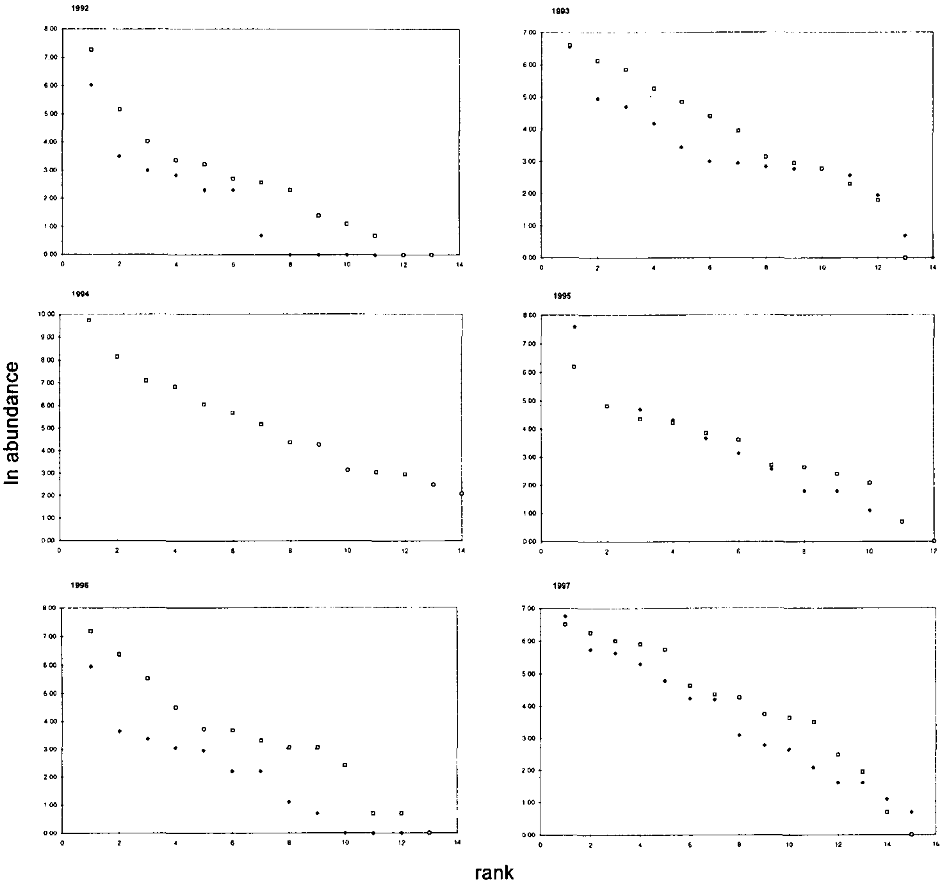

Fig. 5. Rank/abundance plots of the *C. fuscula* parasitoid complex in a crop and its boundary 1992–1997. Based on annual Malaise catches. Filled symbols – boundary; open symbols – crop. Overlapping symbols: 1993 – rank 10; 1995 – rank 2, 11, 12; 1996 – rank 13.

Only four species had higher relative fractions than 10% in both habitats at least once during the six years: the larval parasitoids *D. begini* and *Hemiptarsenus unguicellus*, and the pupal parasitoids *C. vulgaris* and *Chrysocharis pubicornis*. The combined fraction of *C. vulgaris* and *D. begini* in the crop roughly exceeded 70% most years, but was less in 1997 and 1993 (26 and 58%, respectively), when the two other species increased in abundance. A regular pattern appeared between the two dominant larval parasitoids in the crop: the fractions of *H. unguicellus* increased when the fractions of *D. begini* decreased and vice versa, and for both species an increase in one year was always followed by a decrease the next year. On the other hand, the fractions of both the two dominant pupal parasitoids, *C. vulgaris* and *C. pubicornis*, showed an increasing trend in the crop during the period, except for the distinct decrease of *C. vulgaris* in 1997, when it for the first time had a lower abundance than *C. pubicornis* in this habitat.

The pattern of dominant species differed in the two habitats: *C. vulgaris* always dominated the boundary complex, which consisted of 64–90% pupal, 10–27% larval, and 0.2–11% larval-pupal parasitoids. In the crop, however, the dominance alternated between pupal (*C. vulgaris*) and larval (*D. begini*, *H. unguicellus*) parasitoids. Here, the relative abundance of larval, pupal and larval-pupal parasitoids had much greater fluctuations annually: 25–87, 13–68 and 0.2–7%, respectively. In all years, *C. vulgaris* had a higher relative abundance in the boundary (43–83%) than in the crop (10–55%). The high abundance of parasitoids in the grass boundary (1995, early 1996) was mainly due to this species. The other dominating species, *D. begini*, always had a higher and more variable relative abundance in the crop (12–81%) than in the boundary (5–12%).

The sampling periods of the two habitats were different in most years (Table 2). If only including catches from the periods the two habitats had in common each year, parasitoid abundance is considerably reduced some years (1993 and 1995; Table 2: numbers in parentheses). However, reducing the sampling period this way only leads to minor changes (max. 5%) in the relative frequencies given in Table 2. A short sampling period did not necessarily lead to a low parasitoid abundance (e.g. 1994 crop).

Species richness, evenness and diversity in different years and habitats

Species richness (S) was similar in the two habitats (Table 2, Fig. 4), but in 4 of the 5 years with traps in both habitats, crop catches had a distincly higher diversity (H'), and consequently a lower dominance (d'), than boundary ones (Fig. 3). This is reflected in the plots of species rank against ln abundance (Fig. 5): the boundary curves tended to be steeper at small ranks (i.e. the most abundant species) than the crop curves. Median values were $H' = 1.4$ and 1.1, and $d = 0.5$ and 0.7, for crop ($n = 6$ years) and boundary ($n = 5$), respectively. Only small changes in the indices occur if the common sampling period in the two habitats is used instead. A hypothesis of higher diversity in the boundary than in the crop can be rejected if H' is assumed to be normally distributed ($p < 0.05$, one-tailed paired t-test, $t = -2.14$, $n = 5$), but not otherwise ($p = 0.06$, one-tailed Wilcoxon signed rank test, $n = 5$).

It is noteworthy that S and H' were highest in 1993 and 1997, the only years with a distinct F_1 generation of *C. fuscula* (Fig. 4). The indices seemed to vary between years in a similar pattern in the two habitats: e.g. 1997 had the highest diversity in both habitats and 1992 the lowest, but the years are too few to ascertain this (Spearman rank correlation of H' in crop and boundary: $p = 0.23$, $r = 0.7$, $n = 5$).

DISCUSSION

When Malaise catches are used to study the parasitoid complex of a particular host, some important points must be kept in mind:

1. Most trap devices are taxonomically biased. Malaise traps are well suited for collecting small hymenopterans (Darling & Packer, 1988; Noyes, 1989; Gaston & Gauld 1993; Greiler, 1994; Powell et al., 1996), and may even be more efficient than sweep net sampling (Lockwood et al., 1996). In our study of a relatively homogeneous group of chalcid leaf miner parasitoids, Malaise trapping therefore seemed an appropriate method. Still, two unanswered questions are whether the trap efficiency was similar for all parasitoid species and for *C. fuscula* and its parasitoids.

2. The trap efficiency depends on weather conditions like precipitation and temperature (Nyrop & Simmons, 1986). This does not matter when comparing traps that have been in

the same field at the same time, but makes comparisons of total catches between years difficult.

3. In contrast to parasitoid specimens reared from *C. fuscula*, trap collected specimens may have developed on other host species. For instance, *Neochrysocharis aratus* was relatively more common in reared samples (Hågvar et al., 1994) than in the Malaise ones, perhaps because it may be among the most host specific species in the complex (Trandem, 1998c). Another example is *C. vulgaris*, which has a wider host range than *D. begini* (Trandem, 1998c) and therefore might be over-represented in the Malaise traps. Although some inconsistencies between trapped and reared material can be found, both methods clearly point out *C. vulgaris* and *D. begini* as the dominating *C. fuscula* parasitoids in the field studied (Hågvar et al., 1994; Trandem, 1998b). Furthermore, the importance of *C. fuscula* as a host species is implied by high mine densities in the crop (all plants infested in most years) and by the consistency between the catches of the invading *C. fuscula* parental population and the later parasitoid F_1 population.

The lack of an F_1-generation of *C. fuscula* in the catches from most years could be taken to imply that adults of this generation have a different behaviour compared with the parental one that immigrated into the crop. As there was a distinct generation of emerging flies in two of the years, high pre-adult mortality in the other years is a more likely explanation. Such a high mortality is confirmed by dissections (Trandem, 1998a,b). In addition, registrations of *C. fuscula* in the same area and period by yellow water traps and emergence cages showed the same annual pattern with respect to the presence of an F_1 generation as the Malaise catches (A. Andersen, pers. comm.). The mortality can have other causes than parasitism (see Trandem, 1998a for a discussion), but in general, parasitism is the most important mortality factor known for leaf miners in temperate areas (Hawkins et al., 1997).

In contrast to the situation for *C. fuscula*, phenology data (both from the Malaise catches and from reared material; E. Hågvar, T. Hofsvang & N. Trandem, unpubl.) indicated that most parasitoids trapped were of the F_1 generation, emerging from *C. fuscula* and other leaf miners in the crop and its boundaries. The only important exception to this was overwintered *C. vulgaris* females active in the boundary early in the season (Trandem, 1998c). This is the only species in the complex known to overwinter as an adult (Askew, 1965; Trandem, 1998c). The reason why so few parasitoids of the immigrating population were collected in the spring is not clear. Different flight behaviour of the two parasitoid generations could be one explanation, a smaller or more scattered ovipositing population compared to the emerging one could be another.

Both parasitoid and fly catches fluctuated considerably during the six years, probably reflecting real population changes as well as varying trapping conditions. In general, the parasitoid : fly ratio seemed to be higher in the boundary than in the crop, but in total more individuals were caught in the crop than in the boundary, both of *C. fuscula* and parasitoids. Unfortunately, there was no boundary trap in 1994, when the crop parasitoid catch was an order of magnitude bigger than the other years. In the grass boundary in 1995 and spring 1996, the parasitoid catches were also unusually large.

The size of the fly and parasitoid population in the two habitats and the difference between them depended on several factors, among them (not mutually exclusive):

1. The size and survival of the overwintering population.

2. The quality of the boundary (probably more important for the parasitoids than their host) (Altieri et al., 1993): presence of alternative hosts and food for adult parasitoids,

microclimate (e.g. boundary facing north or west), and number of sites for shelter and overwintering.

3. Proximity of boundary to the crop (grass boundary was somewhat closer to the crop than forest boundary, and in 1997 the boundary was not adjacent to the crop).

Considering such factors, we will attempt to interpret some of our results:

If the 1993 fly survival was good in a larger area (as indicated by the emergence of an F_1 generation), a higher fly number than usual might be expected to invade the crops in 1994. This was the case in our crop, since 1994 had the highest F_0 catches of flies during the six years. This in turn would lead to many hosts for the parasitoids, and 1994 also had the highest F_1 parasitoid catch. However, winter survival is also crucial. The winter of 1993–94 had normal temperatures but much snow, which might be positive for the flies by stabilising the local winter temperatures in the ground vegetation layer. Most flies were captured in June, which was not particularly warm or dry in 1994 (Table 1). On the other hand, July and first week of August had the highest temperatures and lowest precipitation registrated during the six years. The extreme number of parasitoids then emerging could be an effect of these favourable conditions in addition to a high host number. Parasitoids were also numerous in the grass boundary catches in 1995 (and early spring 1996), but not in the same boundary in 1997, nor in the early spring in the forest boundary in 1996 (same period as the grass boundary one). These differences might be explained by the high F_1 population of parasitoids in 1994, the grass boundary having better conditions for parasitoids than the forest boundary, and the boundary being closer to the crop in 1995 than in 1997. However, effects of year, prevailing wind, and trees/not trees around the trap cannot be excluded, and the higher parasitoid abundance in the grass boundary (eastern, trap in the open) than in the forest boundary (southern, trap among trees) cannot be attributed to a difference in habitat quality alone without further studies.

The higher abundance of flies and parasitoids in the crop than in the boundary could be explained by higher densities of host plants and hosts in the crop. A larger proportion of parasitoids than flies visited the boundary, also in years with a distinct F_1 fly generation. If this was not due to selective sampling by the trap, our study support previous findings that the majority of the adult *C. fuscula* does not overwinter in the nearest crop boundaries (Andersen, 1991).

The 15 species parasitoid complex of *C. fuscula* here investigated was very stable in species composition and rank abundances through the six years. This was particularly the case in the boundary. The abundance of larval-pupal parasitoids was always low in both habitats. Kato (1994, 1996) found similar characteristics in the parasitoid complex of lowland populations of *Chromatomyia suikazurae* Saksakawa on the forest shrub *Lonicera gracilipes*, which he studied for 10 years in Japan. Like in our crop, the dominance shifted between one larval and one pupal parasitoid (both of the genus *Chrysocharis*). The *C. suikazurae* complex had roughly twice the diversity and half the dominance of the *C. fuscula* one in the present study. Dawah et al. (1995) studied the parasitoid communities associated with endophytic grass-feeding chalcids (*Tetramesa* spp., Eurytomidae) in England and Wales for 13 years, and found a remarkable consistency: the 43 primary parasitoid species or species groups, identified by dissections, had consistent relative abundances in time (and space), perhaps due to the widespread occurrence of all the species. On some of the host species, the parasitoids maintained identical rank abundances throughout the study; while on others the ranked abundances varied substantially.

Comparing the crop and the boundary in the present study, the two habitats had similar species richness. As one very abundant species (*C. vulgaris*) was consistently more dominant in the boundary than in the crop, the former tended to have lower diversity than the latter. This habitat difference was also found in a trap plant experiment in the same study area (Trandem, 1998a). Several reasons may be suggested why the parasitoid diversity was not higher in the boundary than in the crop, contrary to expectation (Altieri et al., 1993; Altieri, 1994):

1. Semi-natural boundaries can increase the arthropod diversity of the nearby crop community (Mayse & Price, 1978; Lewis, 1969; van Emden, 1990), and in a small field like ours, this boundary effect may cover most of the field (Lewis, 1969). Parasitoids are relatively mobile compared to soil surface arthropods (e.g. Marino & Landis, 1996; Hausammann, 1996), in which a boundary effect often has been reported.

2. Our barley crop had a more heterogeneous vegetation than a conventional one, since it was undersown with grass/clover and no herbicides were used. In such a crop, the parasitoid diversity is likely to be higher than in a conventional one (cf. the enemy hypothesis; Root, 1973; Risch et al., 1983) and more similar to boundary conditions. Absence of pesticides is favourable to the parasitoids, both directly (by avoiding toxic effects) and indirectly (by avoiding a kill-off of hosts and other resources, e.g. flowering weeds, Powell, 1986; van Emden, 1990). Jensen (1997) collected hymenopteran parasitoids by emergence traps in a cereal field in Denmark, and found higher species richness and lower dominance in unsprayed than sprayed plots. Greiler (1994) used Malaise traps and suction traps to compare the insect community in set-aside fields in Germany. The Malaise samples showed higher species richness of chalcids in one-year-old fallows sown with clover-grass mixtures than in conventional rye fields. This suggests that the grass/clover in our barley crop enhanced the parasitoid diversity. Coll & Bottrell (1996) demonstrated rather complex differences in migrations and movements of the parasitoid *Pediobius foveolatus* in monocultures (bean) and mixed cropping (bean-maize). Parasitoid abundance was primarily determined by emigration rates, but in the long run the parasitoids accumulated in the most diverse crop.

3. Non-crop habitats may have the greatest significance for parasitoids early in the season, when resources and microclimate are particularly unfavourable in the crop (Dyer & Landis, 1997). Our results were pooled through the season, with relatively few F_0 parasitoids.

4. The diversity was calculated on a selected and limited group of parasitoids on a single host. From what was left of parasitic hymenopterans when the relevant species had been sorted out from the Malaise catches, it seemed obvious that the boundary had a more diverse such fauna than the crop.

Interspecific competition can be important in organising parasitoid communities associated with endophytic hosts when resources are limited (Hawkins, 1990; Hawkins et al., 1990; Kato, 1994, 1996; Sato, 1995; but see Mills, 1993; Godfray, 1994; Dawah et al., 1995). Malaise catches alone cannot prove competition, but we would like to point out some possible indications of competition among the parasitoids in our study:

1. Larval-pupal parasitoids were scarce. Larval-pupal parasitoids are by definition koinobionts (parasitoids allowing their host to develop after parasitization; Askew & Shaw, 1986), and risk being killed by both larval and pupal idiobionts (parasitoids killing or permanently paralysing the host after parasitization). Most of the 15 species in this study were idiobionts (Trandem, 1998c). This fits the pattern reported from more general

studies: idiobionts are found to be more diverse on endophytic hosts than koinobionts, and this is attributed to idiobionts outcompeting koinobionts on such hosts (see Hawkins, 1990; Hawkins et al., 1992; Askew, 1994; Shaw, 1994).

2. In the years with few F_1 flies (i.e. high host mortality), the crop abundance was high for *D. begini* and low for *C. vulgaris*, or vice versa. *C. vulgaris* cannot outcompete larval parasitoids, which kill hosts before they are suitable for pupal parasitoids. Therefore, if the annual shift in dominance between *D. begini* and *C. vulgaris* in the crop was due to competiton, the larval parasitoid *D. begini* gives the premises. Unlike the crop, the boundary had no shifts in species dominance. The explantation could be that the boundary was more attractive to *C. vulgaris* than to *D. begini*, e.g. with respect to overwintering, alternative hosts, food resources etc.

3. In the two years with many F_1 flies emerging (meaning that healthy unparasitized hosts were in surplus), *C. vulgaris* and *D. begini* both had low relative abundances. Correspondingly, the fraction of the larval parasitoid *H. unguicellus* and the pupal parasitoid *C. pubicornis* (1997) increased, perhaps due to released competition from the two dominating species. The data from all the years suggest that the two larval parasitoids *D. begini* and *H. unguicellus* may compete, as their relative abundances were inversely related. However, the relative abundances of *C. vulgaris* and *C. pubicornis* were not inversely related (but see Trandem, 1998b).

In conclusion, the investigated parasitoid complex of C. *fuscula* was rather stable in composition through the six years, and most so in the boundary. The boundary seemed more important for the parasitoids than for their leaf miner host, and was obviously part of the parasitoids' foraging/overwintering area. As such, the boundary can be important for the control of *C. fuscula*.

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REFERENCES

ALTIERI M.A. 1994: *Biodiversity and Pest Management in Agroecosystems*. Food Products Press, New York, 185 pp.

ALTIERI M.A., CURE J.R. & GARCIA M.A. 1993: The role and enhancement of parasitic Hymenoptera biodiversity in agroecosystems. In LaSalle J. & Gauld I.D. (eds): *Hymenoptera and Biodiversity*. CAB International, Wallingford, pp. 257–275.

ANDERSEN A. 1991: Life-cycle of Chromatomyia fuscula (Zett.) (Dipt., Agromyzidae), a pest in Norwegian cereal fields. *J. Appl. Entomol.* **111**: 190–196.

ANDERSEN A. & FUGLEBERG O. 1997: Developmental rates for Chromatomyia fuscula (Zett.) (Dipt., Agromyzidae) at five constant temperatures. *J. Appl. Entomol.* **121**: 311–314.

ASKEW R.R. 1965: The holarctic species of Cyrtogaster Walker and Polycystus Westwood (Hym., Pteromalidae) including the description of a new species of Cyrtogaster from Britain. *Entomophaga* **10**: 179–187.

ASKEW R.R. 1994: Parasitoids of leaf-mining Lepidoptera: what determines their host ranges? In Hawkins B.A. & Sheehan W. (eds): *Parasitoid Community Ecology*. Oxford University Press, Oxford, pp. 177–202.

ASKEW R.R. & SHAW M.R. 1986: Parasitoid communities: their size, structure and development. In Waage J. & Greathead D. (eds): *Insect Parasitoids*. Academic Press, London, pp. 225–264.

Bouček Z. 1965: Studies of European Eulophidae, IV: Pediobius Walk. and two allied genera (Hymenoptera). *Acta Entomol. Mus. Nat. Pragae* **36**: 590.

Coll M. & Bottrell D.G. 1996: Movement of an insect parasitoid in simple and diverse plant assemblages. *Ecol. Entomol.* **21**: 141–149.

Compton S. 1981: The chalcid fauna of the Jostedalen (Hym. Chalcidoidea). *Fauna Norv. (Ser. B)* **28**: 83–89.

Darling D.C. & Packer L. 1988: Effectiveness of Malaise traps in collecting Hymenoptera: the influence of trap design, mesh size, and location. *Can. Entomol.* **120**: 787–796.

Dawah H.A., Hawkins B.A. & Claridge M.C. 1995: Structure of the parasitoid communities of grass-feeding chalcid wasps. *J. Anim. Ecol.* **64**: 708–720.

Dyer L.E. & Landis D.A. 1997: Influence of noncrop habitats on the distribution of Eriborus terebrans (Hymenoptera: Ichneumonidae) in cornfields. *Environ. Entomol.* **26**: 924–932.

Emden H.F. van 1990: Plant diversity and natural enemy efficiency in agroecosystems. In Mackauer M., Ehler L.E. & Roland J. (eds): *Critical Issues in Biological Control.* Intercept, Andover, pp. 63–80.

Gaston K.J. & Gauld I.D. 1993: How many species of pimplines (Hymenoptera: Ichneumonidae) are there in Costa Rica? *J. Trop. Ecol.* **9**: 491–499.

Godfray H.C.J. 1994: *Parasitoids. Behavioral and Evolutionary Ecology.* Princeton University Press, Princeton, New Jersey, 473 pp.

Graham M.W.R. de V. 1993: The identity of some species of Chalcidoidea (Hym.) described by Nees von Esenbeck (1834), with new synonymy. *Entomol. Mon. Mag.* **129**: 221–230.

Greiler H.-J. 1994: Insektengesellschaften auf selbstbegrünten und eingesäten Ackerbracken. Dissertation, Univ. Karlsruhe 1993, Agrarökologie 11, 136 pp. (in German, English abstr.).

Hausammann A. 1996: Strip-management in rape crop: is winter rape endagered by negative impacts of sown weed strips? *J. Appl. Ecol.* **120**: 505–512.

Hawkins B.A. 1990: Global patterns of parasitoid assemblage size. *J. Anim. Ecol.* **59**: 57–72.

Hawkins B.A., Askew R.R. & Shaw M.R. 1990: Influences of host feeding-niche and foodplant type on generalist and specialist parasitoids. *Ecol. Entomol.* **15**: 275–280.

Hawkins B.A., Shaw M.R. & Askew R.R. 1992: Relations among assemblage size, host specialization, and climatic variability in North American parasitoid communities. *Am. Nat.* **139**: 58–79.

Hawkins B.A., Cornell H.V. & Hochberg M.E. 1997: Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* **78**: 2145–2152.

Hågvar E.B., Hofsvang T. & Trandem N. 1994: The leafminer Chromatomyia fuscula (Diptera: Agromyzidae) and its parasitoid complex in Norwegian barley fields. In Hågvar E.B. & Hofsvang T. (eds): Insect Parasitoids: Biology and Ecology. Proceedings from the 5th European Workshop on Insect Parasitoids, May 24–28, Biri, Norway. *Norw. J. Agric. Sci. (Suppl. No. 16)*: 369–378.

Heinz K.M. & Parella M.P. 1990: Holarctic distribution of the leafminer parasitoid Diglyphus begini (Hymenoptera: Eulophidae) and notes on its life history attacking Liriomyza trifolii (Diptera: Agromyzidae) in chrysanthemum. *Ann. Entomol. Soc. Am.* **83**: 916–924.

Jensen P.B. 1997: The influence of unspraying on diversity of soil-related hymenopteran parasitoids in cereal fields. *J. Appl. Entomol.* **121**: 417–424.

Kato M. 1994: Structure, organization, and response of a species-rich parasitoid community to host leafminer population dynamics. *Oecologia* **97**: 17–25.

Kato M. 1996: Effects of parasitoid community structure upon the population dynamics of the Honeysuckle Leafminer, Chromatomyia suikazurae (Diptera: Agromyzidae). *Res. Popul. Ecol.* **38**: 27–40.

Lewis W.J. 1969: The diversity of the insect fauna in a hedgerow and neighbouring fields. *J. Appl. Ecol.* **6**: 453–458.

Lockwood J.A., Shaw S.R. & Struttmann J.M. 1996: Biodiversity of wasp species (Insecta: Hymenoptera) in burned and unburned habitats of Yellowstone National Park, Wyoming, USA. *J. Hym. Res.* **5**: 1–15.

Marino P.C. & Landis D.A. 1996: Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* **61**: 276–284.

Mayse M.A. & Price P.W. 1978: Seasonal development of soybean arthropod communities in east central Illinois. *Agro-Ecosystems* **4**: 387–405.

MILLS N.J. 1993: Species richness and structure in the parasitoid complexes of tortricioid hosts. *J. Anim. Ecol.* **62**: 45–58.

NOYES J.S. 1989: The diversity of Hymenoptera in the tropics with special reference to Parasitica in Sulawesi. *Ecol. Entomol.* **14**: 197–207.

NYROP J.P. & SIMMONS G.A. 1986: Temporal and spatial activity patterns of an adult parasitoid, Glypta fumiferanae (Hymenoptera: Ichneumonidae), and their influence on parasitism. *Environ. Entomol.* **15**: 481–487.

OTTESEN P. 1993: Norske insektfamilier og deres artsantall. [Norwegian insect families and their species numbers.] *NINA Utredning* **55**: 1–40 (in Norwegian, English abstr.).

POWELL W. 1986: Enhancing parasitoid activity in crops. In Waage J. & Greathead D. (eds): *Insect Parasitoids*. Academic Press, London, pp. 319–340.

POWELL W., WALTON M.P. & JERVIS M.A. 1996: Populations and communities. In Jervis M.A. & Kidd N. (eds): *Insect Natural Enemies: Practical Approaches to Their Study and Evaluation.* Chapman & Hall, London, pp. 223–292.

RISCH S.J., ANDOW D. & ALTIERI M.A. 1983: Agroecosystem diversity and pest control: Data, tentative conclusions, and new research directions. *Environ. Entomol.* **12**: 625–629.

ROOT R.B. 1973: Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (Brassica oleracea). *Ecol. Monogr.* **43**: 95–124.

SATO H. 1995: Comparison of community composition of parasitoids that attack leaf-mining moths (Lepidoptera: Gracillariidae). *Environ. Entomol.* **24**: 879–888.

SHAW M.R. 1994: Parasitoid host ranges. In Hawkins B.A. & Sheehan W. (eds): *Parasitoid Community Ecology*. Oxford University Press, Oxford, pp. 111–144.

SOUTHWOOD T.R.E. 1995: *Ecological Methods with Particular Reference to the Study of Insect Populations. 2nd ed.* Chapman & Hall, London, 524 pp.

SUNDBY R. 1957: The parasites of Phyllocnistis labyrinthella Bjerk. and their relation to the population dynamics of the leaf-miner. *Norsk Entomol. Tidsskr. (Suppl. 2)*, 153 pp.

TOKESHI M. 1993: Species abundance patterns and community structure. *Adv. Ecol. Res.* **24**: 111–186.

TRANDEM N. 1998a: The parasitoid complex of the leafminer Chromatomyia fuscula (Dipt.: Agromyzidae): trap plant experiments in a cereal field and its margins. In Trandem N.: *The Parasitoid Complex of Chromatomyia fuscula (Diptera: Agromyzidae) in Spring Barley.* Thesis, Agricultural University of Norway, Ås, 168 pp.

TRANDEM N. 1998b: The parasitoid assemblage and mortality pattern of the agromyzid leafminer Chromatomyia fuscula (Zett.) in spring barley fields at different latitudes. In Trandem N.: *The Parasitoid Complex of Chromatomyia fuscula (Diptera: Agromyzidae) in Spring Barley.* Thesis, Agricultural University of Norway, Ås, 168 pp.

TRANDEM N. 1998c: The biology of parasitoids attacking Chromatomyia fuscula (Zett.) (Diptera: Agromyzidae) in Norway: an overview. In Trandem N.: *The Parasitoid Complex of Chromatomyia fuscula (Diptera: Agromyzidae) in Spring Barley.* Thesis, Agricultural University of Norway, Ås, 168 pp.

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