Relative importance of predators and parasitoids for cereal aphid control

Martin H. Schmidt[1][*], **Andreas Lauer**[1], **Tobias Purtauf**[2], **Carsten Thies**[1], **Matthias Schaefer**[3] and **Teja Tscharntke**[1]

[1]*Department of Agroecology, Georg-August University, Waldweg 26, D-37073 Göttingen, Germany*
[2]*Department of Animal Ecology, Justus-Liebig University, Heinrich-Buff-Ring 26-32, D-35392 Giessen, Germany*
[3]*Department of Animal Ecology, Georg-August University, Berliner Strasse 28, D-37073 Göttingen, Germany*

Field experiments with manipulations of natural enemies of plant-feeding insects may show how a diverse enemy group ensures an important ecosystem function such as naturally occurring biological pest control. We studied cereal aphid populations in winter wheat under experimentally reduced densities of: (i) ground-dwelling generalist predators (mostly spiders, carabid and staphylinid beetles); (ii) flying predators (coccinellid beetles, syrphid flies, gall midges, etc.) and parasitoids (aphidiid wasps), and a combination of (i) and (ii), compared with open controls. Aphid populations were 18% higher at reduced densities of ground-dwelling predators, 70% higher when flying predators and parasitoids were removed, and 172% higher on the removal of both enemy groups. Parasitoid wasps probably had the strongest effect, as flying predators occurred only in negligible densities. The great importance of parasitism is a new finding for aphid control in cereal fields. In conclusion, a more detailed knowledge of the mechanisms of natural pest control would help to develop environmentally sound crop management with reduced pesticide applications.

Keywords: biological control; Aphidiidae; Araneae; *Sitobion avenae*; winter wheat; parasitism

1. INTRODUCTION

Top-down regulation of herbivores is more likely in ecosystems with few species and little heterogeneity in space and time, as suggested by models and recent meta-analysis of field studies (Hawkins *et al.* 1999; Schmitz *et al.* 2000). Despite their temporal instability, annual crops are terrestrial habitats in which predators can exert the strongest regulation of herbivore populations, and where herbivores may cause the highest levels of plant damage when predators fail to control them (Halaj & Wise 2001). Yet herbivore–natural enemy interactions in winter wheat, which is the dominant crop in many temperate areas, are still not sufficiently understood to predict pest outbreaks. The lack of knowledge of the relative importance of control agents and their interactions contributes to this unpredictability (Sunderland *et al.* 1997; Fagan *et al.* 1998; Lang 2003).

The herbivore community of winter wheat in Germany is dominated by three species of cereal aphids (*Sitobion avenae* (Fabricius), *Metopolophium dirhodum* (Walker), *Rhopalosiphum padi* (Linnaeus)), which cause economic damage in some years, and against which insecticides are commonly applied. Several groups of natural enemies may limit aphid populations: adults and larvae of ladybirds (Coccinellidae), larvae of hoverflies (Syrphidae), gall midge larvae (Cecidomyiidae) and lacewing larvae (Chrysopidae) live in the upper vegetation of cereal fields and feed predominantly on aphids (Wratten & Powell 1991). Parasitoid wasps (Hymenoptera: mainly Aphidiidae) occupy the same stratum and are specialized on one or several aphid host species (Sigsgaard 2002).

Ground-dwelling predators such as spiders (Araneae), carabids (Carabidae) and rove beetles (Staphylinidae) have a much wider prey spectrum, but include aphids in their diet and are able to suppress their numbers (Symondson *et al.* 2002). The relative abundances of the natural enemies vary widely among years and study sites. There are published records of successful aphid control by all of them, but their relative importance and interactions are little known, because most field studies deal with only one group. Thus it is necessary to experimentally study the effect of several enemy groups at the same time (Winder *et al.* 1994; Sih *et al.* 1998; Lang 2003).

We compared the relative impact of different natural enemies on aphid population development in a two-factor field experiment. The predation effect under natural densities was compared with treatments where either ground-dwelling predators or flying predators and parasitoids were reduced singly and in combination. We expected that these two groups have an effect on aphid population growth, and that the generalist predators were most important early in the season, whereas specialist predators and parasitoids, which respond numerically to aphid abundances, would have their highest impact at high aphid densities late in the season (Kromp 1999; Marc *et al.* 1999).

2. MATERIAL AND METHODS

The experiments were carried out in 2001 in four insecticide-free winter wheat fields, representing varied site conditions typical for the area. The field cultivation was carried out by the Reinshof research farm of Göttingen University in Lower Saxony, Germany. Two of the fields were situated in a structurally rich landscape with nutrient-poor calcareous soils and a high

[*]Author for correspondence (m.schmidt@uaoe.gwdg.de).

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1905

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diversity of land-use types. The other two fields lay in a structurally poor, crop-field dominated landscape in the Leine valley on deep, nutrient-rich loamy soils. In each landscape, one field was conventionally managed (structurally poor landscape: field 2; structurally rich landscape: field 4), and one was managed according to the European Union Regulation 2092/91/EEC on organic farming, without artificial fertilizers and pesticides (structurally poor landscape: field 1; structurally rich landscape: field 3). The experimental treatments were applied in a 2×2 factorial design with six replications of ground-dwelling predator removal ($-G$), flying predator + parasitoid removal ($-F$), complete removal (the combination of both; $-G-F$) and open control (0) in each field. Experimental plots were circular with a diameter of 1 m, resulting in a plot area of 0.79 m². For the removal of ground-dwelling predators, plastic barriers reaching 10 cm into the soil and projecting 30 cm over the surface were set up in early May to reduce the exchange with the surrounding field. One 'live' pitfall trap with a circular opening of 8.7 cm diameter was placed in each barrier, and operated on 13 days throughout May and June. Ground-dwelling predators (spiders, carabids, rove beetles and ants) captured in these live traps were identified and removed. All other animals were returned into the experimental plot. Additionally, web-building spiders were removed manually six times during May and June. The webs were made visible with starch powder (Toft *et al.* 1995), spiders individually removed with a pooter, identified and released outside the plot. To test for the effectiveness of the web spider removal, spider webs were counted in all treatments in field 1 on 17 July, 1 day after the cages had been removed and aphids had been counted. Flying aphid predators and parasitoids were reduced by setting wire cages over the plots at the end of June. The cages had a mesh size of 8 mm to avoid changes in microclimate and were covered with sticky glue to deter or capture flying arthropods (see Müller & Godfray 1999). The bottom edge of the cages was left without glue, and gaps resulting from the uneven soil surface gave ground-dwelling predators access. To test whether the cages had a relevant effect on the microclimate, daily minimum and maximum temperature (T) and relative humidity (h) were measured on 10 consecutive days within and outside a wire cage. t-tests for matched pairs yielded no detectable differences (synchronous measurements as pairs; $T_{min} = 11.64 \pm 0.66$ versus 11.74 ± 0.63 °C, $t = -1.58$, d.f. = 9, $p = 0.148$; $T_{max} = 28.01 \pm 1.71$ versus 28.80 ± 1.65 °C, $t = -1.22$, d.f. = 9, $p = 0.254$; $h_{min} = 63.0 \pm 3.9$ versus $61.2 \pm 5.0\%$, $t = 0.41$, d.f. = 9, $p = 0.689$; $h_{max} = 100.0 \pm 0\%$ in both cases).

Aphids and all natural enemies were counted visually in all treatments on 20 (first date, wheat flowering, 21–26 June 2001) and 40 (second date, milk ripening, 14–18 July 2001) wheat shoots per plot, respectively, before the installation of the wire cages, and three weeks later, after the cages had been removed. Parasitized aphids (mummies) were taken to the laboratory, to rear and identify the parasitoids. Parasitism was calculated as the ratio of mummies to total aphids. Counts of aphids were converted into individuals per 100 shoots. Aphid densities were analysed by ANOVA, including the factors field (1–4), ground-dwelling predator removal (1–2 = yes–no) and flying predator plus parasitoid removal (1–2 = yes–no). The skewness of the data was compensated either by $\log_{10}(x + 1)$-transformation of arthropod densities or arcsine-transformation of aphid parasitism. In addition, the relation of aphid population growth (difference between the two counting dates) to percentage parasitism was analysed by simple regressions. All statistical treatments were performed using the STATISTICA for Windows package 5.5 (StatSoft Inc., Tulsa, USA).

3. RESULTS

Overall, we found 4715 aphids, of which 89.7% were *Sitobion avenae*, followed by *Metopolophium dirhodum* (7.9%) and *Rhopalosiphum padi* (2.4%). Aphid infestations averaged 73.6 individuals per 100 shoots, well below the threshold level of economic damage (five per shoot; Giller *et al.* 1995). The open-field population densities for aphids and their natural enemies are summarized in table 1. Aphid-eating gall midges (Cecidomyiidae, *Aphidoletes* cf. *aphidimyza* (Rondani)) were only abundant in field 1 with 31.0 ± 4.7 individuals per 100 shoots, without significant differences between treatments. In the other three fields, these gall midges occurred only with 0.5 ± 0.2 individuals per 100 shoots. Spiders were the next most numerous predator on the vegetation, with on average 5.3 ± 0.5 individuals per 100 shoots. Larvae of lacewings (Chrysopidae; 0.14 ± 0.09 individuals per 100 shoots) and ladybirds (Coccinellidae; 0.04 ± 0.04 individuals per 100 shoots) were rare, and aphid-eating larvae of hoverflies (Syrphidae) were not encountered at all.

With pitfall traps, 603 carabids, 393 rove beetles, 10 ants (Formicidae) and 580 spiders (309 Lycosidae, 238 Linyphiidae and 33 Tetragnathidae) were removed from treatments $-G$ and $-G-F$ at 13 dates during May and June. Another 2439 spiders were removed manually at six dates through web search. These were dominated by the subfamily Linyphiinae (80.6%), followed by Araneidae plus Tetragnathidae (11.3%), Erigoninae (5.3%), and Theridiidae (2.7%). The initial density of spider webs on 17 May was 10.9 ± 0.9 m^{-2}, without significant differences between fields. On 17 July, at the end of the experiment, web abundance in field 1 was 41.2% lower in the ground predator removal ($F_{1,20} = 18.7$, $p < 0.001$), and unaffected by the flying predator removal ($F_{1,20} = 0.27$, $p = 0.61$). In the un-manipulated plots 95.6 ± 9.2 webs per square metre covered some $10.6 \pm 1.3\%$ of the ground surface.

Aphid densities at wheat flowering showed no significant treatment effects ($-G$: $F_{1,80} = 0.46$, $p = 0.50$; $-F$: $F_{1,80} = 1.56$, $p = 0.21$). They differed between fields ($F_{3,80} = 7.65$, $p = 0.0001$), ranging from 30.8 ± 9.1 individuals per 100 shoots in field 3 to 71.9 ± 8.5 individuals per 100 shoots in field 4. By the end of the experiment (milk-ripening stage), the removal of ground-dwelling predators led to a 44.4% increase in aphid populations ($F_{1,80} = 4.0$, $p = 0.048$), whereas the removal of flying predators and parasitoids led to an increase in aphid densities of 102.8% ($F_{1,80} = 38.2$, $p < 0.0001$). Aphid densities were 17.9%, 69.8% and 172.0% higher in the treatments $-G$, $-F$ and $-G-F$, respectively, compared with open controls (figure 1). There was no significant interaction between the removal treatments ($-G \times -F$: $F_{1,80} = 2.0$, $p = 0.16$). The effect of ground-dwelling predators varied between fields, being marked only in fields 1 and 4 (interaction $-G \times$ field: $F_{3,80} = 2.8$, $p = 0.048$).

Parasitism of aphids by wasps (Aphidiidae) increased from $1.8 \pm 1.1\%$ on the first sampling date to $18.4 \pm 1.5\%$ on the second date (for absolute densities, see table 1). On the second date, parasitism differed

Table 1. Ambient (unmanipulated) densities of aphids and their natural enemies in the experimental fields.

(Aphids, parasitoids and flying predators: individuals per 100 shoots, $n = 24$ plots (treatment 0). Web spiders: individuals per square metre, $n = 48$ plots (17 May; treatments $-G$ and $-G-F$ before manipulation) and $n = 12$ plots (17 July; treatment 0 and $-F$; field 1 only). Other ground-dwelling predators: individuals captured per unenclosed pitfall trap on 13 days through May–June, $n = 24$ traps (six per field). Arithmetic means ± standard errors.)

		21–26 June	14–18 July
aphids	*Sitobion avenae*	39.2 ± 11.7	59.2 ± 5.7
	Metopolophium dirhodum	16.9 ± 4.4	0.4 ± 0.2
	Rhopalosiphum padi	1.7 ± 1.3	0.1 ± 0.1
parasitoids	Aphidiidae[a]	0.8 ± 0.8	15.6 ± 2.6
flying predators	*Aphidoletes* cf. *aphidimyza* (larvae)	10.4 ± 4.8	13.1 ± 5.4
	Araneae[b]	4.6 ± 1.4	6.8 ± 0.8
	Chrysopidae (larvae)	0	0.1 ± 0.1
	Coccinellidae (larvae)	0	0

		17 May	17 July
ground-dwelling predators	web spiders[c]	10.9 ± 0.9	95.6 ± 9.2

		May–June
	cursorial spiders[d]	20.5 ± 2.0
	Carabidae	22.1 ± 1.8
	Staphylinidae	8.2 ± 1.5

[a] Aphid mummies: mostly *Aphidius*, hyperparasitized by *Asaphes* (Pteromalidae) and *Dendrocerus* (Megaspilidae).
[b] Individuals associated with shoots: mostly Linyphiidae and Theridiidae.
[c] Mostly *Tenuiphantes tenuis* (Linyphiidae) and *Bathyphantes gracilis* (Linyphiidae).
[d] *Pardosa* sp. (Lycosidae) and *Pachygnatha degeeri* (Tetragnathidae).
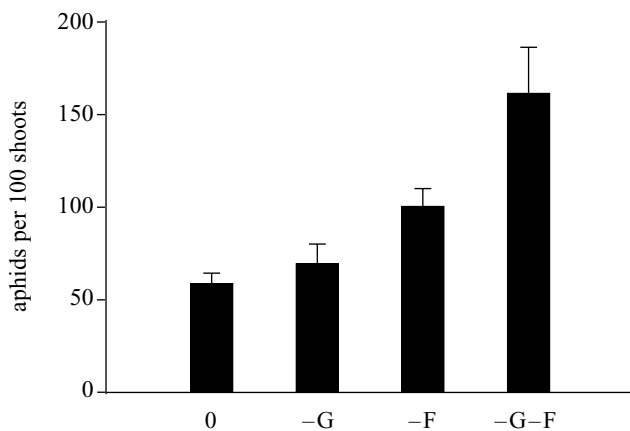

Figure 1. Aphid densities at the end of the experiment (milk ripening). 0, open control; $-G$, ground-dwelling predator removal; $-F$, flying predator and parasitoid removal; $-G-F$, removal of all predators and parasitoids.
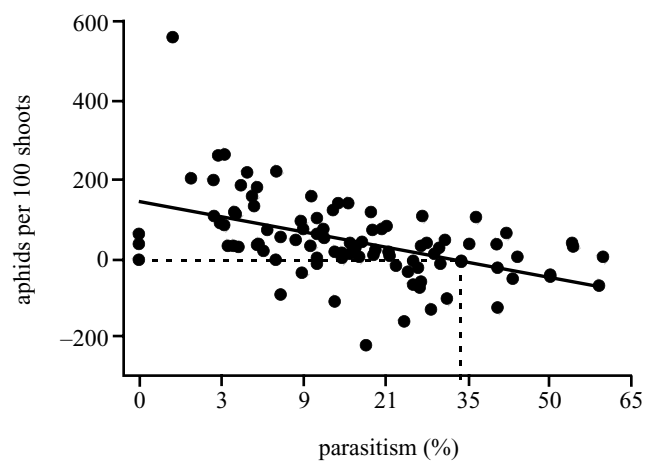

Figure 2. Correlation between aphid population growth (the difference in aphid density between wheat flowering and milk ripening) and (arcsine-transformed) parasitism. $r = -0.49$, $n = 96$ plots, $p < 0.001$. $y = 149 - 3.8x$.

significantly between fields ($F_{3,80} = 13.8$, $p < 0.001$), with higher values in the structurally rich landscape (24.5 ± 2.3 versus $12.4 \pm 1.6\%$), but no obvious differences between organic and conventional management (18.5 ± 2.4 versus $18.3 \pm 1.9\%$). Parasitism was 56.4% lower in the flying predator and parasitoid removal treatment than in controls (11.2 ± 1.3 versus $25.6 \pm 2.2\%$; $F_{1,80} = 40.85$, $p < 0.001$), and tended also to be reduced by ground-dwelling predator removal (16.0 ± 2.0 versus

$20.8 \pm 2.2\%$; $F_{1,80} = 3.18$, $p = 0.078$). The development of aphid populations correlated negatively with parasitism (figure 2), but not with predator densities. Aphid populations decreased between wheat flowering and milk ripening at parasitism rates higher than 33%. The negative correlation between aphid population growth and parasitism was present in every field, and hence was not an artefact of field-specific differences (field 1: $r = -0.51$,

$n = 24$ plots, $p = 0.01$, $y = 193 - 6.9x$; field 2: $r = -0.47$, $n = 24$ plots, $p = 0.02$, $y = 93 - 2.4x$; field 3: $r = -0.58$, $n = 24$ plots, $p = 0.003$, $y = 167 - 3.2x$; field 4: $r = -0.74$, $n = 24$ plots, $p < 0.001$, $y = 223 - 6.6x$). Sixty-eight per cent of the aphid mummies reared in the laboratory contained hyperparasitoids.

4. DISCUSSION

The experimental manipulations showed that both groups of enemies are able to reduce cereal aphid population growth. The effect of flying predators plus parasitoids was stronger than that of the ground-dwelling predators. As the abundance of flying predators was very low, parasitoid wasps were likely to have provided the most important contribution towards suppression of aphid densities in the treatments in which they occurred at natural densities. The reduced parasitism in the patches where the flying predators and parasitoids were removed, and the overall negative correlation between aphid population growth and parasitism support this finding. At parasitism levels above 33%, aphid densities decreased between the two sampling dates. This rate is within the threshold value of 32–36%, below which success in classical biological control has never been found (Hawkins & Cornell 1994). Few other studies report similarly high parasitism of cereal aphids (e.g. Sigsgaard 2002), and only Levie *et al.* (2000) found regulation of cereal aphids by parasitoids released into field cages. To the best of the authors' knowledge, the study presented here is the first field experiment that gives evidence for a control of cereal aphids by naturally occurring parasitoid wasps. Fluctuations in population density, abiotic stress factors, hyperparasitism and intraguild predation of parasitoids by predators may prevent the effectiveness of parasitoids in many situations (Sunderland *et al.* 1997). The high levels of hyperparasitism that we found did not appear to prevent an effective control of cereal aphids by their primary parasitoids during the time-period examined, although hyperparasitism has been shown previously to reduce the effectiveness of primary parasitoids (Rosenheim 1998).

Many studies show that ground-dwelling generalist predators may reduce pest numbers (Symondson *et al.* 2002), but several in European winter wheat revealed only weak, temporary or no effect (Holland *et al.* 1996; Holland & Thomas 1997; Lang 2003). Theoretical considerations, and some experimental evidence, suggest that the effects of ground-dwelling predators on aphids should be strongest as early as May, when aphid densities in cereals are low and reproduction is slower than in summer (Chiverton 1986; Kromp 1999; Marc *et al.* 1999; Lang 2003). Our study revealed an effect of ground-dwelling predators in July, which may be attributable to the fact that mostly linyphiid spiders were manipulated. Their abundance peaks in July, when the densities of other ground-dwelling predators have already declined.

Multiple enemy species may act synergistically on their shared prey (Völkl 1992; Hoelmer *et al.* 1994; Losey & Denno 1998; Colfer & Rosenheim 2001). By contrast, intraguild predation, and particularly predation of parasitized pests, may disrupt biological control (Rosenheim *et al.* 1995; Sunderland *et al.* 1997; Raymond *et al.* 2000). Our results indicate that the dominant web spiders and

parasitoid wasps complement each other. The removal of ground-dwelling predators tended to reduce parasitism, hence strong intraguild predation appears unlikely. Aphids get caught in linyphiid webs when they drop from the vegetation, a behaviour also shown to escape from *Aphidius* wasps (Longley & Jepson 1996). The immobility of aphid mummies should preserve them from spider predation. This may explain why the generalist predators in our study did not interfere with parasitoids. By contrast, vegetation-climbing carabids may prefer mummies to non-parasitized aphids and thereby disrupt biological control by parasitoid wasps (Snyder & Ives 2001).

Entomophagous arthropods are expected to benefit from diversification within the field and at the landscape level (owing to diverse food sources, places for hibernation, and shelter from the disturbances caused by agricultural practices; Altieri *et al.* 1993; Wratten & van Emden 1995; Thies & Tscharntke 1999; Sunderland & Samu 2000). In accordance with this hypothesis, we found higher parasitism in the structurally rich landscape but, unexpectedly, no differences between conventional and organic management. However, more landscape and management replicates are necessary to verify these relations.

In conclusion, the role of parasitoid wasps in the control of cereal aphids has to be reconsidered. They appeared to be more important than ground-dwelling generalist predators, and the effects of both groups were complementary. More field experiments should compare the relative impacts of different aphid natural enemies under the varied relative abundances at which they occur in the field. Also, more knowledge is needed about factors that determine their population densities, including landscape, climate and management. Biological pest control becomes increasingly important, as public opinion is in favour of reduced pesticide applications and environmentally sound cereal production (Tilman *et al.* 2002). Farming schemes could further promote and benefit from naturally occurring aphid enemies.

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